

University of Alberta

**Fire Skips and Understory Plant Diversity in
an Upper Foothills - Subalpine Forest in
Northwestern Alberta**

Quinn W. Bottorff



A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of Master of Science

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Spring 2001



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-60414-4

Canada

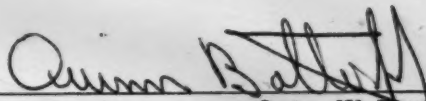
University of Alberta

Library Release Form

Name of Author: Quinn W. Bottorff
Title of Thesis: Fire Skips and Understory Plant Diversity in
an Upper Foothills - Subalpine Forest in
Northwestern Alberta
Degree: Master of Science in Forest Biology and
Management
Year this Degree Granted: 2001

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly, or scientific research purposes only.

The author reserves all other publication and other rights associated with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

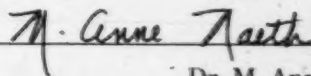

Quinn W. Bottorff
#8, 1665 Edson Drive
Edson, Alberta, Canada
T7E 1G6

Date: July 17, 2000

University of Alberta

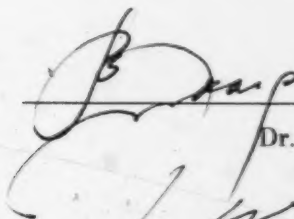
Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Fire Skips and Understory Plant Diversity in an Upper Foothills - Subalpine Forest in Northwestern Alberta submitted by Quinn W. Bottorff in partial fulfillment of the requirements for the degree of Master of Science in Forest Biology and Management.

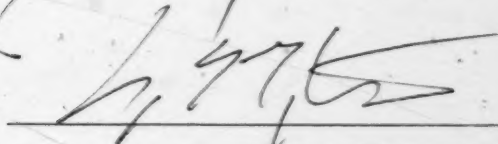


Dr. M. Anne Naeth

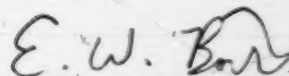
Supervisor



Dr. Paul M. Woodard



Dr. Luigi Morgantini



Dr. Edward Bork

Date: July 17, 2000

DEDICATION

To my parents Brian and Faye, simply thank you.

ABSTRACT

The objectives of this study were to classify and describe the understory plant communities of a burned area, associated fire skips and adjacent unburned forest in an upper foothills - subalpine region of northwestern Alberta and to determine the role of fire in this classification. The understory vegetation from 44 samples was separated into 6 community types by TWINSpan and corresponding community types using Detrended Correspondence Analysis. Fire was the primary controlling factor in determining understory species composition and abundance. Changes in environmental conditions due to canopy closure are responsible for further changes in understory plant species composition and abundance. Larger fire skips (>1.5 ha), including their non edge affected core communities, riparian communities and edge communities, probably represent distinct understory plant communities on the landscape. These results may have implications for subalpine forest management.

ACKNOWLEDGMENTS

First and foremost, I would like to thank Weyerhaeuser Company Ltd - Canada. and all their staff, especially Dr. Luigi Morgantini, for supporting this project financially and for their time and effort. A special thanks to the Weyerhaeuser Company Ltd. - Canada helicopter staff, Gene and Bruce, for everything especially the pizza and pop, which made our summer field season more bearable. Without the strength, diligence and organization of my field staff, Greg Greidanus, Michelle Christenson and Ted Harms and my fellow graduate student Kamal Ghandi and her field staff, this project would not have been possible. I would also like to thank those who helped me organize my field season and assisted with my data analysis: Dr. Emmanuel Mapfumo, Dr. David Chanasyk, Dr Mark Dale, Dr. John Spence and his field staff, Dr. Peter Blenis, Dr. Francis Yeh, Treena Fenniak, Alex Drummond, Don Page, Mae and Lisa.

Thanks to my other committee members, Dr. Paul Woodard and Dr. Edward Bork, for their continual guidance and support. A generous thanks to the non-academic staff of the Department of Renewable Resources for their assistance with everything from registration to computer support. A special thought goes out to all my fellow graduate students who have lent a hand and touched my life over the past 3 years; there are too many of you to list, but you know who you are.

A special thanks to my supervisor Dr. Anne Naeth, whose encouragement, patience and kindness not only made this thesis possible but helped me to grow as a person more than I can ever thank her for. For my parents, Brian and Faye Bottorff, my sister Adrienne Bottorff and my grandparents, Lillian and Albert Hareuther thanks for accepting the late nights, the tears and for the serenity. Lastly, for my fiancé Kim Munkler, you are my love and my strength.

TABLE OF CONTENTS

I. Literature Review	1
1.0 Preface	1
1.1 Introduction	1
1.2 Fire in Subalpine Forests	2
1.2.1 The Role of Weather in Subalpine Forest Fire Regimes	5
1.3 Fire and Fire Skips	5
1.4 Ecology of the Understory of Northern Forests	9
1.4.1 Response of Understory Vegetation Immediately After Fire	11
1.4.2 Later Succession of the Understory after Fire	14
1.4.3 Successional Mechanisms of Vascular and Non-Vascular Plants	16
1.4.4 Edge Effects and Understory Plant Communities	18
1.5 Possible Ecological Roles of Fire Skips	19
1.6 Implications for Northern Forest Management	23
1.7 Summary	25
1.8 Objectives	26
1.9 References	26
II. Fire Skips and Understory Plant Diversity in an Upper-Foothills Subalpine Forest in Northwestern Alberta	35
2.0 Introduction	35
2.1 Materials and Methods	38
2.1.1 Study Area	38
2.1.2 Experimental Design	39
2.1.3 Treatments	40
2.1.4 Field Measurements	40
2.1.5 Data Analysis	42
2.2 Results	45
2.2.1 TWINSpan Classification	45
2.2.2 Summary Table	47
2.2.3 Ordinations	49
2.2.4 External Factor Summary	51
2.2.5 Similarity Analysis	52
2.2.6 Diversity Size Relationship	52
2.2.7 Riparian Areas	53
2.3 Discussion	53
2.3.1 Multivariate Analysis	53
2.3.2 Similarity Analysis	58
2.3.3 Diversity Size Relationship	59
2.3.4 Riparian Areas	60
2.3.5 Implications for Forest Management and Future Research	60
2.4 Conclusions	61
2.5 References	62

LIST OF TABLES

Table 2.1 Number and corresponding sizes of fire skips in the study site.....	69
Table 2.2 Description of treatments and corresponding number of samples and sub-samples.....	69
Table 2.3 Description of samples (transects) used in DCA analysis.....	70
Table 2.4 Average cover for measured species.....	71
Table 2.5 Summary of understory plant species cover and other environmental factors in the 6 community types from TWINSpan.....	75
Table 2.6 Results of the forward selection of ordination centroids ("treatments") from a CCA with their approximate significance, and canonical coefficients and intraset correlations for the first two axes.....	79
Table 2.7 Summary of understory plant species cover and other external factors for the 7 stratified treatment types.....	79
Table 2.8 Euclidian Dissimilarity Indices comparisons.....	80
Table 2.9 Euclidian Dissimilarity Indices comparisons between the burned area, large, medium and small skip cores and edges.....	80
Table 2.10 Latin and common names of understory plant species.....	81

LIST OF FIGURES

Figure 2.1	Orthophoto of study site.....	85
Figure 2.2	Close up of fire skips (Orthophoto).....	86
Figure 2.3	Diagram of treatment sampling (Not to scale).....	87
Figure 2.4	Dendrogram of community types (groupings) obtained by TWINSpan.....	88
Figure 2.5	DCA biplot of all 44 samples and selected centroids. Circles delineate samples according to sample groupings and treatment type. Same circles used in Figure 2.6.....	89
Figure 2.6	DCA biplot of selected centroids (from Figure 2.5), 12 external factors and species*. External factors use scale A while scale B used for centroids and species.....	90
Figure 2.7	Linear regression of species richness of skips versus size of skips (95% Confidence Interval).....	91
Figure 2.8	Linear regression of Shannon-Weiner species diversity versus size of skips (95% Confidence Interval).....	91
Figure 2.9	Linear regression of species evenness of skips versus size of skips (95% Confidence Interval).....	92

I. LITERATURE REVIEW

1.0 Preface

In this chapter, the literature pertinent to this study is reviewed. It begins with a general introduction of the relevant fire literature and then proceeds to a review of fire regimes and fire behaviour in foothills and subalpine areas, where this particular study took place. It then reviews the literature pertaining to the formation of fire skips and the ecology of understory plant species after fire, which are the foci of this study. Considering this literature, the possible ecological roles of fire skips in understory plant ecology are examined, including community organization, diversity and succession. The implications of the ecological roles of fire skips on forest management are also examined. Finally, the objectives of this study are stated, which focus on the role of fire skips in maintaining understory plant species diversity.

1.1 Introduction

Disturbance is one of the primary forces, which determine the patterns observed on the landscape. In the forests of the circumpolar north, the primary natural disturbance has been fire (Heinselman 1971, Rowe 1961, White 1979, Wright and Bailey 1982, Wein and Maclean 1983, Johnson 1992). The type, intensity, duration, severity and extent of fire determine the post fire composition and succession of the flora and fauna of northern forests (Heinselman 1971, Tande 1979, Foster 1983, Payette et al. 1989, Keane et al. 1996). However, fire regimes are not consistent across the northern forests and vary spatially and temporally among and within regions (Heinselman 1973, White 1979, Wright and Bailey 1982, Wein and Maclean 1983, Foster 1983, Payette et al. 1989, Rogeau 1996, Andison 2000).

Fires and fire regimes in northern forests vary with a number of factors including weather, climate, vegetation, age and other physiographic features; with estimates for the incidence of stand replacing fires ranging from 50 to 600 years (Rowe 1961, Mutch 1970, Dix and Swan 1971, Heinselman 1973, Zackrisson 1977, Tande 1979,

Romme and Knight 1981, Foster 1983, Foster and King 1986, Barret et al. 1991, Bergeron 1991, Johnson 1992, Bessie and Johnson 1995). Many examples of how these features interplay and modify fire regimes in northern forests are found in the literature.

For example, in southeastern Labrador, areas dominated by lichen woodlands or paper birch (*Betula papyrifera* Marsh.) require frequent fires for their perpetuation on the landscape (Foster 1983, Foster and King 1986). In contrast, areas dominated by spruce woodlands only have a fire return period of 500 years. This low fire return period is probably due to high levels of precipitation. These areas are located on an interior plateau with many fire breaks; mainly peatlands and water bodies which further inhibit the spread of fire. Paper birch dominated areas are located in the watersheds of various rivers where the topography is quite steep allowing for the frequent spread of stand replacing fires (Foster 1983, Foster and King 1986). In comparison, the fire history of islands within Lake Duparquet was compared to that of the lakeshore in northern Quebec. The morphology and location of the islands resulted in both a higher frequency of fires and fires of more variable intensity compared to the lakeshore, which was dominated by lethal, high intensity fires. This has probably resulted in the perpetuation of pine species (*Pinus* sp.) on the islands (Bergeron 1991).

1.2 Fire in Subalpine and Foothills Forests

This study was conducted in the mountainous (above 4900 feet) upper foothills and subalpine natural regions of Alberta that are dominated by coniferous forests and are characterized by snowy cold winters and showery cool summers (average of 558 to 752 growing degree days, 538 to 568 mm mean annual precipitation) (Beckingham et al. 1996). The upper foothills region is located anywhere 900 to 1500 m above sea level with lodgepole pine (*Pinus contorta* Loudon) stands dominating, however, white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) are considered the climax tree species. The subalpine natural region is located at elevations above that of the upper foothills, and below that of alpine natural region, anywhere from 1300 to 2000 m above sea level. In those areas

with more precipitation, mixed Englemann spruce / subalpine fir (*Picea englemannii* Parry ex Engelm. / *Abies lasiocarpa* (Hook.) Nutt.) stands dominate (Strong and Leggat 1981) and are considered the climax species, while lodgepole pine is found on drier sites and is considered a seral tree species. The compliment of understory species between the natural regions is quite similar, but heathers (*Ericaceae* spp.) and certain shrubs, become more dominant in the subalpine (Beckingham et al. 1996).

Fire regimes in this region of northwestern North America are just as variable as other northern forest types, but some patterns do emerge in the relevant literature. Tande (1979) found that for the period 1665 to 1975 the maximum fire return interval in lodgepole pine dominated areas of Jasper National Park is 31 to 88 years. The minimum fire return interval is 1 to 16 years, with the mean being 27 years. The areas studied were located in the upper foothills, subalpine and montane regions of the park, and were affected by a combination of frequent low intensity fires and infrequent medium to high intensity stand replacing fires. This fire regime resulted in various patterns on the landscape. Where fire was intense enough to cause continuous crown fires, most commonly on upper slopes, even-aged stands result, because all the dominant overstory trees are killed. Low to medium intensity fires result in areas with at least two age classes and are most often located in valley bottoms. Areas of rugged terrain result in forests with many age classes over short distances due to rapid changes in moisture gradients. Some areas have such low intensity fires that the occurrence of fire scars is common, but concurrent tree regeneration is missing whereby the dominant overstory trees are not killed by the fire. In general, ground fires of low to medium severity are common in drier areas. Less frequent, but large stand replacing fires are more common in moist areas due to greater fuel accumulation. However, large stand replacing fires do occur in both moist and dry areas (Tande 1979, Arno 1980).

These results are similar to those of Romme and Knight (1981) for a lodgepole pine dominated subalpine forest in Wyoming. Periodic high intensity fires and slow succession maintain lodgepole pine on upper slopes, while areas on valley bottoms with less frequent intense fires and more rapid succession are dominated by

Englemann spruce / subalpine fir forests. Upland areas without fire for over 400 years have succeeded to Englemann spruce/subalpine fir forests, indicating that these are the climax species in foothills and subalpine areas (Romme and Knight 1981, Rogeau 1996). This is confirmed by Arno (1980) who reports that the fire return interval for Englemann spruce/subalpine fir areas is less than those areas nearby dominated by lodgepole pine. In the absence of fire, Loope and Gruell (1973) report the invasion of lodgepole pine by subalpine fir in Wyoming, but that successional dominance may take several hundred years. The researchers also reported that lodgepole pine areas sheltered from frequent fires can become dominated by Englemann spruce over 200 to 500. Keane et al. (1996) used an ecological process model and found that shade-tolerant species, such as Englemann spruce and especially subalpine fir, tend to dominate Rocky Mountain landscapes only when fire is excluded.

For a fire in an Englemann spruce dominated forest, Fryer and Johnson (1988) relate many of the same dominant factors found by Tandé (1979) and Romme and Knight (1981). Like most fires in the subalpine, the 1936 Galatea fire caused almost total canopy mortality, with 92% of the area burnt. The areas that survived were located close to a river, at right angles to the passage of the fire or upwind of the fire. The forest tree composition remained the same after the fire, indicating that fires maintain species composition and inhibit succession.

More recently, Andison (2000) studied landscape level fire activity in the eastern slopes of the Rocky Mountains in Alberta finding the average fire cycle for the upper foothills natural region was 89 years, and 69 years for the lower foothills natural region. The average age was 76 years for the lower foothills and 82 years for the upper foothills, and 111 years for the subalpine natural region. Andison's results indicate different burning regimes for these three natural regions with the amount of lightning, burning conditions and topography responsible. However, from the data and models Andison used, age class distributions in this landscape are not stable and the amount of area in various seral stages for each of these natural regions range widely.

The results of Anderson confirm those of Rogeau (1996) who found significant variability in age class distributions in the southern Canadian Rocky Mountains. Rogeau's results indicate that the Weibull and negative exponential models are not appropriate for estimating fire cycles in the Rocky Mountains, primarily because the fire cycle varies spatially in mountain landscapes. Variations in the landscape over large areas indicate that smaller areas with similar landscapes have similar fire cycles and the fire cycles for these smaller areas cannot be applied to the entire larger landscape.

1.2.1 The Role of Weather in Subalpine Forest Fire Regimes

Fryer and Johnson (1988) found that the fuel in the Galatea fire area became extremely dry during a blocking high pressure system, which preceded the fire. Lightning ignited the fire when this system weakened. The three major fire runs also occurred when this system weakened, which results in high and variable winds. Fire reconstruction indicated that weather, not fuel type or elevation, was a more important factor in determining fire behaviour in subalpine conditions. Bessie and Johnson confirmed these results, by finding weather was typically responsible for causing high intensity versus low intensity fires in subalpine forests. Using the fire behaviour models of Rothermel (1972) and Van Wagner (1977), Bessie and Johnson found surface fire intensity and crown fire initiation were most strongly correlated to weather rather than fuel. Moreover, larger burned areas had higher fire intensity predictions than smaller areas. Bessie and Johnson explain that during years where large areas burned the weather variable shifted to more extreme values, lowering the relative importance of fuels; in turn, resulting in most of the stands achieving the threshold necessary for crown fire initiation. This supports the theory that fire intensity and severity are determined primarily by extreme variations in weather, rather than fuel variations associated with stand age.

1.3 Fire and Fire Skips

Most fires in Alberta, including those in subalpine areas, are less than 200 ha in size, however, the 3% of fires that are greater than 200 ha are responsible for 95% of

the total area burned (Eberhart and Woodard 1987, Strauss et al. 1989). Although these larger fires may have increased capacity for damage because of increased size and severity, they are not homogeneous in composition. Rarely is all the vegetation within the fire perimeter burned. Patches of overstory and understory vegetation are left within the larger burned area and these patches can range in size from a clump of a few trees to tens of hectares (Eberhart and Woodard 1987). Others have referred to these areas as residuals, stringers or swamp forests (Quirk and Sykes 1971, Eberhart and Woodard 1987, Hornberg et al. 1998). In this thesis these areas will be referred to as fire skips.

Several hypotheses can account for the formation of fire skips, but no definitive study on this topic has been completed, especially for northern mountainous regions. Hornberg et al. (1998) reviewed research from 13 boreal swamp forests in Sweden over a decade. On average, the mean fire return interval of these swamp forests was over 400 years compared to 50 to 180 year intervals for surrounding forests. Many swamp forests are true fire free refugia, having never actually been burned. Most of these areas are located in low areas where the risk of ignition by lightning is low and the continuous wet conditions lower the risk of a severe fire associated with increased fuel accumulation. These continuous wet conditions also promote the reproduction and growth of hydrophilous species, which do not desiccate, further lowering the risk of ground fires spreading from drier surrounding forests. Moreover, when fire does occur, the variability of microhabitats within swamp forests creates an irregular fire pattern compared to adjacent uplands. Human intervention in prehistoric times included selective cutting, grazing by domestic animals, burning and deliberate flooding, which has affected both ecological structure and function of these areas.

Quirk and Sykes (1971) discovered unburned patches of 200-year-old white spruce surrounded by areas of 34-year-old white spruce. These stringers were found in depressions in the topography, where there was a sudden change in slope on the landscape. Quirk and Sykes (1971) hypothesized these changes in micro-relief may have shielded these fire skips. These depressions also had 21.3% higher soil moisture content by volume in the surface horizon compared to the younger forest.

Some of the fire skips contained intermittent streamlets, suggesting moisture might play a role in the formation of fire skips.

Other researchers have speculated that variations in topography and wind, and the locations of wetlands and water bodies may also affect the formation of fire skips (Heinselman 1973, Rowe and Scotter 1973, Eberhart and Woodard 1987, Bergeron 1991). Fryer and Johnson (1988) found the areas that survived a crown fire in the subalpine were located near a river. It has also been suggested that fire skips form downwind of fuel breaks such as bare rock or soil, or other features that interrupt the fuelbed (Foster 1983, Eberhart and Woodard 1987). Van Wilgen et al. (1990) discovered that forested patches surrounded by shrublands in South Africa were much less likely to burn when both areas were threatened with the same fire. The forested areas were less susceptible to fire because they had higher moisture contents, lower crude fat contents of leaves and branches, and the litter and canopy layers more were separated.

In the boreal forest of Ontario, Van Wagner (1967) found that foliar moisture content differed considerably for both deciduous and conifer species during the growing season. In a related experiment, wetter leaves produced less radiant heat than dry leaves when burned. Chrosciewicz (1996) studied the variations in foliar moisture content of new and old growth over two growing seasons for several coniferous species. Chrosciewicz found that the moisture content in old foliage declined in the early spring, new foliage had its highest moisture content when the old foliage had its lowest moisture content and the moisture contents of both converged from then on over the summer. This trend was similar for two years but foliar moisture content was sensitive to long dry periods and varied with foliar age. These two studies reveal that foliar moisture content, weather and age could have a significant impact on the flammability of individual trees and on the subsequent likelihood of a crown fire. Correspondingly, areas that are continually moister, such as those discovered by Quirk and Sykes (1971), could be favoured for the formation of fire skips, or for the perpetuation of already existing fire skips on the landscape

because of sustained elevations in foliar moisture content, regardless of the age of the trees, the weather or the age of the foliage.

These theories are corollaries of a hypothesis of Mutch (1970), whereby fire dominated communities burn more often and freely than non-fire dominated communities because natural selection has favoured development of characteristics which make them more flammable. If this flammability caused a competitive advantage over other non-fire adapted species then fire-adapted species could dominate in fire prone areas. Plant characteristics that fire could select for include thick bark, underground perennating organs and protected seeds which actually lessen the damage due to fire; a corollary of Mutch's hypothesis. Another corollary of Mutch's hypothesis is that fire selects for traits which maximize regeneration efficiency such as the development of fire stimulated seed-fall and germination, seedling dependence on ground cover clearance or ashbed nutrient enhancement (Buckley 1984). Sylvester and Wein (1981) found extreme differences in the flammability of many arctic plant species. Therefore, in addition to other factors such as topography and weather, fire skips may not burn because their plant species do not inherently favour being burned compared to those in surrounding stands. However, Snyder (1984) believes that fire is not a major force in natural selection and that other forces, possibly in conjunction with fire, are responsible for these traits.

Usually, more fire skips of larger sizes are found after larger fires because smaller fires might not be large enough, or burn long enough to encounter conditions that would lead to the formation of fire skips. Eberhart and Woodard (1987) found classes E1 (201 to 400 ha) and E2 (401 to 2,000 ha) fires contained significantly more fire skips than class C (20 to 40 ha) or D (41 to 200 ha) fires. Class E3 (2,001 to 20,000 ha) fires had fewer fire skips per area than either class E1 or E2 fires, but the increase in the size of the E3 fire skips compensated for the decrease in E3 fire skip numbers. They also discovered that the larger the fire, the greater the maximum distance from the edge of the forest to the fire skip, and that larger fires have a greater edge index and a greater fire shape index.

1.4 Ecology of the Understory of Northern Forests

Although studies of the role of fire skips in the ecology of understory species, mosses, lichens, grasses and forbs, have not been completed, many papers have been published on the understory ecology of boreal forests of North America. Fire changes the factors that affect understory species growth and reproduction in a complex fashion and the biotic and abiotic interactions that influence post fire effects are not fully understood (Pyne et al. 1996). Wright and Heinzelman (1973) summarized the general effects of fire on plant communities where fire may selectively eliminate part of the understory plant community and alter seedbeds by removing litter and humus and creating areas of bare soil. Fire may directly affect plants by triggering the release of seeds in some species or stimulating flowering and fruiting of many shrubs and herbs. This influences germination and survival of many forest species. Moreover, fire stimulates vegetative reproduction of many woody and herbaceous species when the overstory is reduced. Sprouting from roots, root collars and lignotubers is common (McLean 1969). Fire temporarily reduces competition for moisture, nutrients, and light, thereby selectively favouring some species. Fire frequency influences community composition and successional stage and controls overstory age for vegetation types experiencing crown fires. Lastly, fire frequency regulates susceptibility of forests to blowdowns.

These results are the response of vegetation to changes in both abiotic and biotic environmental factors. Differences in the size and shape of the gap created by fire effect the burned understory, especially if the overstory tree canopy was removed, as in a crown fire. Associated with canopy removal are an increase in light, and a change in the quality of light reaching the understory community (Collins et al. 1985). The effects of fire on soil vary with the fuel, soil and the fire, especially fire severity and timing. Therefore, fire can influence soil temperature, soil structure and soil water holding capacity. In particular, fire has dramatic effects on the water repellency, erosion potential, nutrient regime and the microbial community of soil (Pyne et al. 1996).

In interior Alaska, Dyrness et al. (1989) found that the soil chemistry among four forest types, white spruce, black spruce, paper birch and trembling aspen (*Populus tremuloides* Michx.), differed soon after fire. Fire reduced nitrogen (N) in white spruce, paper birch and quaking aspen stands, but actually raised available N in heavily burned black spruce stands. Potassium, calcium and magnesium amounts remained the same after fire, except in heavily burned stands, while soil pH remained constant. Available phosphorus severely dropped in black spruce stands after fire, but increased in aspen and white spruce. The researchers concluded that fire caused short-term changes in soil chemistry, although the duration of these changes is not known. In a pine forest in Israel, Kutiel and Naveh (1987) found that total N decreased by 25% after fire, but that available forms of N were much higher. Other nutrients increased after fire as well, resulting in an increase in shoot and root biomass.

In a 160-year chronosequence in Glacier National Park, Alaska, Bormann and Sidle (1990) found that as stands became dominated by Sitka spruce (*Picea sitchensis* Bong.) from Sitka alder (*Alnus sinuata* (Reg.) Rybd.), soil N decreased. They associated the dominance of Sitka spruce and decreasing soil N with an increase in productivity and above ground biomass. Eventually, more and more nutrients accumulated in the soil organic matter. These results are similar to those of Pare et al. (1993) for a 231-year chronosequence in the boreal forest of Quebec. The forest floor accumulated organic matter and total nutrients, while available P and K decreased, but available N did not. In a related study of the same chronosequence, Brais et al. (1995) found that pH, cation exchange capacity (CEC), Ca, Mg and K all decreased with time, while NO₃ and NH₄ did not decrease during succession.

Baath et al. (1995) found that total microbial biomass decreased in a Norway spruce (*Picea abies* (L.) Karst) dominated stand in northern Finland after fire, with fungal populations being more severely affected than bacterial populations. Clearcutting followed by burning in the same forest type raised soil pH, CEC and base saturation compared to the surrounding unharvested forest (Pietikainen and Fritze 1995). Total microbial carbon also decreased after cutting and burning with the greatest decrease in the fungal community. The researchers speculate that changes in the

structure of the soil humus are responsible for these decreases, with high respiring pioneer bacteria dominating the soil after burning.

Collins et al. (1985) place plants, which respond to gaps created by fire, in three categories: sun herbs, light flexible herbs and shade herbs. All three categories respond differently to fire because of their inherent genetic capabilities. Sun herbs have a metabolism adapted to high intensity light environments, while shade herbs are physiologically adjusted to low light environments and may even reveal photolability. Light flexible herbs are photosynthetically plastic over a range of light intensities and can change their metabolisms to respond to increases in light intensity. This gives them advantages over both sun and shade herbs in response to fire.

1.4.1 Response of Understory Vegetation Immediately After Fire

The response of understory vegetation immediately after a fire in northern forests seems to correlate primarily to fire severity, but results vary according to many factors. Revegetation of a disturbed area is principally from buried seed and/or underground parts located within the burned area, or from seed transported to the burned area after the fire (Ahlgren 1960, Zasada 1971, Johnson 1975, Moore and Wein 1977, Chapman and Crow 1981).

Schimmel and Granstrom (1996) found that the colonizing understory species in the Swedish boreal forest were correlated with fire severity, whereby initial mortality increased with depth of burn. Rhizomatous species were nearly eliminated when the fire burned through to the mineral soil, while species which reproduced by seed had a higher survival rate in these severe burns. Rhizomatous species were more successful immediately after moderate fires, but not severe fires. Differences in plant communities correlated with depth of burn were still evident after five years, indicating that fire severity could have a long lasting impact on understory vegetation.

These results are consistent with other researchers. Schaeffer (1993) found that burned areas in the Manitoba boreal forest are rapidly dominated by species whose

reproductive propagules survived fire and that these species reproduced vegetatively rather than by seed. Flinn and Wein (1977) report that vegetatively reproducing species whose propagules are located in the litter layer, or F and H layer will not survive low intensity or slightly severe fires. Species whose vegetative propagules are located in the mineral soil will survive most fires and will have a competitive advantage over other plants that must establish from seed.

Archibold (1978) studied germination following fire with results contradicting those of the previous studies. He found only 13% of individuals germinating from soil cores taken from a fire originated from remnant root material, while the majority of colonizing species germinated from seed. Like the other researchers, Archibold found rapid revegetation of the burn site was possible, indicating northern forest species are well adapted to fires. The germinant population included herbs, shrubs and early successional tree species. Germination was higher in cores taken from the moderate burn, than from either the unburned forested areas or heavily burned areas, further indicating that northern forest species could be adapted to light to moderate fires. Similar results are reported by Woodard (1977) for burned soil cores taken from lodgepole pine stands in the Cascade Mountains of Washington State.

In a subarctic forest, Johnson (1975) reported very low numbers of viable buried seed in the soil due to immediate germination after seed drop, or due to predation. Therefore, recovery of burned areas in the subarctic is due to perennial tubers sprouting in the soil of the burned area, or from immigrant seeds. Moore and Wein (1977) reported that the majority of viable seed was located in the upper organic layers of soil in several New Brunswick forests. This seed could easily be removed by fires of low severity, indicating that less viable seeds from deeper in the mineral profile would be responsible for colonization of the burned area. However, Moore and Wein reported that deeply buried seeds could even be susceptible to lethal heat from an intense and severe fire.

Granstrom (1987) reported a wide variability in the ability of seed from different species to remain dormant for five years in a mature coniferous forest soil of northern Sweden. Most of the species that did not remain dormant and were

therefore not viable, germinated in the first and second years. However, the species whose seeds survived the five years in the soil were viable at the end of the experiment and would be available to colonize a burned site. Martin et al. (1975) report that both moist and dry heat increased seed germination in a number of different legume species, indicating fire could possibly have a positive result for some seed reproducing species.

In the Superior National Forest in Minnesota, understory species found in only unburned areas consisted of vegetatively reproducing perennial, shade tolerant herbs whose reproductive parts were either destroyed by the fire, or could not compete with light adapted species (Ahlgren 1960). The species only found on burned areas were mainly seed reproducing annuals. These seed producing species invaded the burned area by wind or animals, while only a few vegetatively reproducing species survived the fire and were found in the burned area after the fire. Seed reproducing species dominated severely burned, moist areas, where vegetatively reproducing species would have been eliminated and conditions favoured germination. The species found in both unburned and burned areas reproduced by seed or vegetatively and were the most common species in the study area. These mainly herbaceous species exhibited tolerances for both fire and shade, and provided lush vegetation for the first two years after fire. These light flexible herbs remained dominant for several years in the burned area after the fire until woody species started to dominate (Ahlgren 1960).

Armour et al. (1984) found that the pre-burn understory plant community was similar to the post-burn community. Abundance of most species was uniform under both high and low intensity fires. Graminoids increased in canopy coverage and not in density after fire, while total forb cover remained constant with only small changes in composition. The change in graminoid abundance was due to fire severity, whereby more severe fires killed the rhizomes of graminoid species.

Similarly, in an oak (*Quercus rubra* L.) forest of New York, understory species, which reproduced from rhizomes in the litter, were more successful at reproduction after fire (McGee et al. 1995). These species increased in frequency and cover for 8 to

12 years after a prescribed burn, compared to species with rhizomes in the mineral soil or those that reproduced from seeds. McGee et al. found very few seed colonizing species that survived 8 to 12 years after burning. The understory community composition was not significantly affected by burn severity and was similar to the pre-burn community.

McLean (1969) summarized the relationship between root system characteristics and the relative fire resistance of understory species for a Douglas-fir (*Pseudotsuga menzeii* (Mirb.) Franco) forest in British Columbia. Species that produce stolons or rhizomes above the soil are susceptible to fire, while moderately resistant species produce fibrous roots with rhizomes 5 cm below the mineral soil surface. Resistant species are those with rhizomes located between 5 and 13 cm below the soil surface or those with taproots which are able to regenerate from below their crowns.

1.4.2 Later Succession of the Understory after Fire

Some debate exists about whether seed reproduction or vegetative reproduction is more successful after fire. This depends on the species composition of the community involved and the severity of the fire, among many other factors. Vascular plant species that reproduce vegetatively on the burned site and those that produce large amounts of seed to rapidly invade the site should usually dominate. Michalsky (1987) found that most plants recovered after a prescribed burn in a subalpine region in Alberta, except for trees and shrubs. After one year post-fire species composition was very similar to that of the pre-fire species composition, with grass and sedge cover increasing after fire and forb cover initially decreasing but recovering after one year. No other literature pertaining to the survival, reproduction and recolonization of subalpine or foothills understory species in Alberta immediately after fire and during subsequent succession of these communities afterwards could be found. However, many examples on the succession of understory species in other northern and northwestern forest ecosystems exist in the literature.

Halpern (1988 and 1989) and Halpern and Franklin (1990) studied understory vegetation changes in two clearcut and slash-burned Douglas-fir dominated watersheds in the western Cascade Mountains of Oregon. Immediately after disturbance there was a rapid floristic change within the communities, somewhat dominated by invaders. However, a majority of predisturbance species persisted after the disturbance. As succession continued there was a gradual, unidirectional return to the predisturbance community, whereby change was characterized by shifts in the abundance of the persistent species. Variations in disturbance intensity (burn severity) resulted in the greater dominance of invasive species in more severely disturbed areas and a longer successional period for the return of these areas to predisturbance composition. The stability of these communities is related to the tolerance of understory dominants to burning and their ability to perennate from below-ground structures, like roots, root collars, rhizomes, corns, bulbs, tubers and lignotubers (Chapman and Crow 1981). Their results indicate both deterministic factors (life history traits of colonizing species) and stochastic factors (disturbance intensity, site factors-seed availability, stand history) influence vegetation succession.

In the southern boreal forest of Quebec, the long-term succession of understory species coincided with the succession of deciduous tree species to coniferous species (Bergeron and Dansereau 1993, DeGrandpre et al. 1993). An increase in coniferous species in the canopy coincided with a decrease in richness, diversity and evenness of shade intolerant vascular plant species. However, these results concurred with those reported in the previous section, whereby the majority of the vascular species were present throughout succession. Some non-vascular species were not found in disturbed areas and researchers concluded these species required specific conditions to reestablish. Approximately 150 years into succession a spruce budworm (*Choristoneura fumiferana*) outbreak created openings in the canopy. These openings were associated with an increase in the abundance of early successional species and an increase in understory species richness and diversity (Bergeron and Dansereau 1993).

Dix and Swan (1971) found that late successional tree species of the western boreal forest were limited to balsam fir (*Abies balsamea* (L.) Mill.) and white spruce. Balsam fir is found in the understory of most dominant overstory tree species that originally pioneered the area, and white spruce is found in the understory of trembling aspen and paper birch. Associated with each of the dominant tree species was a particular complement of understory species. Similar to the results of DeGrandpre et al. (1993), there was a marked decrease in understory species diversity as balsam fir became dominant in the canopy. However, Carleton and Maycock (1980) found that many common understory species were unresponsive to dramatic canopy changes in the James Bay area.

The vascular plant succession after fire in the black spruce forests of southeastern Labrador, near Inuvik in the Northwest Territories and in northern Quebec were similar to that reported previously. However, non-vascular species succession was markedly different than that of vascular species (Black and Bliss 1978, Foster 1985, Morneau and Payette 1989). Many vascular species rapidly regenerated vegetatively after fire and grew quickly using the favourable post-burn environmental conditions and the only changes documented were in the size and/or abundance of these species for repeated fire sequences. These same species remain in the understory as succession continues. A few species were eliminated after fire because of susceptibility to fire itself or associated changes in environmental conditions. In contrast, non-vascular (cryptogam) succession followed physiognomic trends as one group of non-vascular species replaced another as succession continued and had a well defined successional pathway after each fire (Black and Bliss 1978, Foster 1985). Morneau and Payette (1989) explained that lichen and moss species exhibited a replacement pattern as the burned area recovered and the tree canopy began to close.

1.4.3 Successional Mechanisms of Vascular and Non-Vascular Plants

An explanation for the succession of vascular understory species can be derived from Anderson et al. (1968). In the pine forests of Wisconsin, the herb layer was responsive to both light and throughfall precipitation, as determined by canopy

opening. Greater canopy opening resulted in increased light penetration and increased throughfall precipitation, which in turn resulted in increased total leaf area in the understory vegetation. The researchers believed that the understory was more responsive to throughfall precipitation than light because the understory herbs were rooted in the upper mineral soil and lower litter layer, and thicker litter layers were associated with increased canopy closure and greater interception of throughfall precipitation. This would further limit the amount of moisture reaching the soil-litter interface and thus, limit herb growth.

Collins et al. (1985) noted that understory species respond not only to changes in light and moisture, but also to changes in temperature, nutrients and even wildlife species within gaps. As these conditions change, vascular plant species that were already present and recovered vegetatively only change in abundance and size in response to these changing conditions. Many invader species that regenerate by seed seem to be eliminated, or extremely reduced within the conflagration area. Carleton et al. (1985) found that for vascular species that recover immediately after fire vegetatively (and non-vascular species), the primary factors determining understory composition and succession were soil related factors, with increasing canopy and stand age as secondary factors. Many researchers remark that vascular plant species succession follows the initial floristic model of Egler (1954) and the tolerance and inhibition model of Connell and Slatyer (1977). The majority of species present before disturbance remain after disturbance, and once they colonize a site they can hold it against all new invaders, and are also tolerant of changing environmental conditions within the burned area as succession continues.

Shafi and Yarranton (1973) are among the few researchers who report that vascular and non-vascular plant succession follow relay floristics in the boreal forest of Ontario. However, the results of Dix and Swan (1971) could be interpreted as a relay floristics as well. Succession in the model Shafi and Yarranton occurs in four phases: initial heterogeneity, early phase, heterogeneous phase and late phase. Initial heterogeneity is due to the spatial variation in fire severity and to the heterogeneity in pre-fire vegetation. Early phase is more homogeneous due to the understory plants, which rapidly dominate the site. As more species invade the

burned area and competition increases, spatially the area becomes more heterogeneous. Late phase begins with canopy closure and shade tolerant species dominating the understory. In all areas studied, succession varies spatially, but areas become more homogeneous in abundance and cover as succession continues. In the boreal forest of Manitoba, spatial heterogeneity did not decrease with succession, and no continual increase in spatial scale with floral succession was discovered. Areas regenerating after fire were rapidly dominated by vegetative reproducing species that survived the fire and dominated sites for at least five years (Schaeffer 1993).

Non-vascular plant species (lichens and mosses) succession in northern forests seems to follow the relay floristic model of Egler (1954) and the facilitation model of Connell and Slatyer (1977). As habitats become more stable, the environment less severe and habitats become diversified, different species of non-vasculars become established (Foster 1985). Foster (1985), Black and Bliss (1978) and Morneau and Payette (1989) comment that the most important factors that change with succession are tree establishment and growth. Associated with this is an amelioration of temperature and moisture extremes, decrease and changes in the quality of light and increased humidity experienced by both tree species and understory species. For both vascular and non-vascular species, regardless of which successional model is suitable, succession is due to the individualistic behaviour of species, which operate within a different set of morphological and physiological limits. Moreover, these same species then grow and reproduce within environmental regimes that vary both spatially and temporally (Collins et al. 1985, Foster 1985).

1.4.4 Edge Effects and Understory Plant Communities

Many researchers comment that edges resulting from fires, harvesting or other disturbances can alter understory communities in forested areas (Hoehne 1981, Levenson 1981, Ranney et al. 1981, Matlack 1994). Matlack (1994) found that edge species primarily favour light-oriented environmental gradients (litter, moisture and temperature), which results in a distinct microclimate in edge areas. This orientation was greatest immediately after the removal of standing trees resulting

in expanding herb, shrub and tree populations due to increased opportunities for vegetative propagation and seedling recruitment. These edge effects lasted until the overstory canopy at the edge had completely closed (Matlack 1994). Edge effects could even alter the understory species composition of small areas of standing trees as the entire plant community could be affected by light-oriented environmental gradients.

The results of Matlack (1994) are similar to those of Hoehne (1981), Levenson (1981) and Ranney et al. (1981) who all studied forested islands in agricultural and urban landscapes in southern Wisconsin. Levenson (1981) found that the richness of these islands is a function of disturbance and that richness increased until islands reached a size of 2.3 ha. Richness decreased until island size reached 3.8 ha because the interiors of these islands represented characteristic plant species of the original forests, without many of the invasive and non-native plant species found in the edge dominated areas. Islands smaller than 2.3 ha functioned essentially as edge communities without the shade tolerant species found in larger islands.

Ranney et al. (1981) found that edge areas of islands were approximately 15 m in width and structurally distinct from the interiors of islands. Edge areas have richer tree species composition, with tree species that are intermediate to intolerant of shade and having increased basal area and density. If islands are small, less than 5 ha in size, these tree species often dominate the interior communities as succession continues. Hoehne (1981) specifically studied understory species and found greater species diversity in the forested patches than in the completely forested areas of the past due to the invasion by weedy and exotic species. Also, many native plant species have decreased in frequency and abundance, or have even been eliminated from these islands due to the invasion of weedy and exotic species, continual disturbance and an overall reduction in total available habitat.

1.5 Possible Ecological Roles of Fire Skips

Although many researchers have studied the understory of the boreal forests, the ecological role of fire skips has not been investigated. Rowe and Scotter (1973),

Ranney et al. (1981), and Eberhart and Woodard (1987) speculate that fire skips could be a potential source for natural reforestation, especially in larger fires where some of the burned area is more than 100 m from the edge of the burned area. This is especially true in severe fires where the fire can kill many of the plant propagules located in the burned area prior to the fire, or if the species is not capable of releasing seed deep into the burned area, such as white spruce (Greene and Johnson 2000). The researchers also speculate that fire skips could harbour bird and ungulate species and provide habitat subsequent to the fire (Eberhart and Woodard 1987).

Hornberg et al. (1998) found that swamp forests (ecologically similar to fire skips) were biodiversity hotspots in the boreal forest of Sweden, containing many rare species of vascular plants, bryophytes, lichens and insects. Even though swamp forests contained no endemic species they did contain up to 60% of all vascular forest plant species, while they only represent 5% of the total forested area of Sweden. A study of 10 remnant areas of a total of only 20 hectares in size contained 517 vascular and non-vascular plant species, with bryophyte diversity being the greatest in these areas.

The researchers comment that these areas are biologically diverse compared to the surrounding forest because of their long fire free intervals, stand continuity and especially a multitude of ecological niches along a hydrotopographical gradient, ranging from dry hummocks to water-filled hollows. These areas contain certain old growth characteristics compared to the surrounding forest, such as large amounts of dead and downed wood in various states of decay and trees of many sizes and ages indicating continuous regeneration, both of which increase the structural and biological diversity of the forest due to increased habitat niches. Another distinguishing feature of these forests is that they are not fire dependent for their continuation on the landscape, unlike many other boreal forest types. Because these areas are unique in the landscape they may be the only areas where many rare species survive and reproducing, act as sources for these rare species. Therefore these areas need to be considered in forest management.

Considering these studies in the boreal forest, fire skips in the subalpine and upper foothills could have similar structural and biological diversity. Initially, fire skips should be a source of plant propagules for shade intolerant and invasive understory species that recolonize the burned area, especially if the burned area is large in size, depending on the successional stage of the skip itself. Fire skips could also contribute rare shade intolerant and invasive species that may not be able to migrate into the burned area from the surrounding forest in sustainable numbers. Fire skips would therefore contribute to an initial increase in plant diversity.

Skips could also harbour understory species that would not survive in the burned area immediately after the fire (Hoehne 1981, Ranney et al. 1981, Hornberg et al. 1998). As succession progresses and conditions in the burned area change, these species could migrate opportunistically into the burned area and enhance its long-term biological diversity (Rowe and Scotter 1973, Hornberg et al. 1998). Patches could serve as additional wildlife habitat for animals that subsequently influence the dispersion of plant propagules into the burned area over time. Without the fire skips these plant species may not become part of the burned area's successional progression.

By increasing both the richness and type of understory species that could migrate into burned areas immediately after the fire and during succession, fire skips contribute to the structural diversity and ecological niches of burned areas. As could the old growth characteristics of many fire skips, especially dead and downed wood (Hornberg et al. 1998). However, the productivity and seed production of initial colonizing species and especially, later successional species within the fire skip, could be altered due to the edge effects resulting from fire (Matlack 1994). Light based edge effects could either inhibit or enhance the understory species ability to contribute plants to the burned area by affecting the ability of understory species to reproduce. Edge effects could even alter the understory species composition of some fire skips, especially smaller fire skips or long thin fire skips in which the entire fire skip would be altered by topographical and light oriented environmental gradients.

Regardless of edge effects, pre-fire understory species composition was similar to that of the post-fire understory species composition in northern forests. Very few colonizing species survive in burned areas for more than 12 years and the species in the burned areas correspond to the severity of fire (Ahlgren 1960, Zasada 1971, Johnson 1975, Moore and Wein 1977). A more severe fire results in more of the upper organic layers of the soil being burned and eliminated. Therefore those species whose reproductive propagules reside in the upper organic layers could be lost from the plant community (Ahlgren 1960, Zasada 1971, Johnson 1975, Moore and Wein 1977, Schimmel and Granstrom 1996). The pattern of understory species found in the burned areas should correlate to the depth of organic matter based on where the various plant propagules are located within that organic matter.

In contrast, the understory plant species composition of the skips could be substantially different than the pre-burned forest because of differences in moisture regime, the presence of wetlands, or differences in topography (Quirk and Sykes 1971, Rowe and Scotter 1973, Bergeron 1991, Hornberg et al. 1998). Therefore, the understory species found in some fire skips might not have the ability to provide colonizing understory plant species to adjacent burned areas as succession continues.

Larger fire skips will likely be better sources of residual plant material during succession because larger fire skips likely contain more habitat niches. Many researchers have found a correlation between island size and species richness and diversity, whereby larger islands have a greater species richness and greater species diversity because of increased habitat niches (Lack 1969). In the same study islands had less bird and floral species than equivalent areas of mainland. Moreover, extinctions occur more often on smaller islands due to a lack of habitat niches (Lack 1969, Brown 1971). Lack (1969) and Brown (1971) focused on large oceanic islands and mainly on animal species, but their results could correspond with smaller facsimiles of islands, such as fire skips.

Levenson (1981) found that a minimum size for an island to maintain its initial tree species composition and act as refugia is 4 ha, while Ranney et al. (1981) found that

this minimum size should be 5 ha. At these sizes and above, edge areas form distinct, diverse communities of shade intolerant understory and overstory communities around interior communities containing many shade tolerant species. Below these sizes, especially islands less than 2.3 ha in size, the interior areas become completely dominated by shade intolerant edge species because of light-oriented edge effects, which effect the entire island (Hoehne 1981). Greene and Johnson (2000) found that even small fire skips (0.095 ha-0.146 ha) could substantially contribute to tree recruitment within large burned areas. This recruitment is important for species like white spruce, whereby tree recruitment into larger burned areas for this tree species would be poor if it only occurred from the edges of the fire.

1.6 Implications for Northern Forest Management

Criticism of the forest industry and its harvesting practices in Canada has increased in recent years due to pressure from self-proclaimed environmentalists, European markets and provincial Forestry Departments (Bondrup-Nielsen 1995). Recently, as issues such as deforestation, fragmentation and the potential loss of biodiversity have entered the public arena, criticism has increased even further. In response, the forest industry has advocated ecologically based forest management practices which are designed to mimic natural disturbances and inherent landscape patterns, such as windfall and insect outbreaks, but especially fire (Swanson and Franklin 1992, Bondrup-Nielsen 1995, Hunter 1993).

Understanding the role of fire skips in maintaining or enhancing plant community diversity and succession of northern forests could provide direction to forest planning. Green tree retention and patch retention harvesting systems are supplied as ecologically based forest management practices to follow at the stand level (Arnott and Beese 1997). It has been recognized that biotic structures, such as standing trees, patches and snags, play a role in the persistence and recovery of ecosystems after a disturbance such as fire (Swanson and Franklin 1992, Arnott and Beese 1997, Acker et al. 1998). At the landscape level researchers such as Hunter (1993), Cumming et al. (1996) and Gauthier et al. (1996) have provided models

based on natural fire regimes upon which to establish these "ecological based forest management" practices.

By better understanding the role of fire skips in the natural disturbance regime, the value of patch retention in cut-overs could be assessed at the stand level. If fire skips do increase the initial and long-term biological and structural diversity of burned areas, then patches could play a similar role in cut-overs. If larger fire skips are more adept at harbouring and therefore increasing the biological diversity of burned areas, then correspondingly patch sizes could be modified.

Not only is it important to understand the role of fire skips in the ecology of subalpine and foothills forests, but it is also important to identify the differences between fire and harvesting on the understory of forests. In the Cascades of Washington, the plant understory was compared among an 8.1 ha clearcut, an 18.7 ha dispersed green tree retention harvest and the surrounding forest (North et al. 1996). The green tree retention (GTR) and the clearcut were contiguous and were harvested in 1992. Both species richness and evenness of the understory (herbs and shrubs) were significantly greater in the GTR than in either of the other two treatments. However, species composition of the GTR was closer to that of the clearcut. The GTR retained more species and cover of shade-tolerant plants that were important for maintaining understory diversity as the overstory canopy closed. Nutrient losses were limited in the partial harvesting systems compared to the clearcut system (Arnott and Beese 1997). Arnott and Beese also found that in a comparison of green tree retention, patch cuttings, uniform shelterwood and clear cutting that harvesting costs were 12% greater for green tree retention and patch cutting treatments and 49% greater for the shelterwood treatment relative to clear cutting.

Noble et al. (1977) found that the understory species composition of logged areas was more similar to that of virgin uncut forests than those effected by wildfire. However, Carleton and MacLellan (1994) found differences in the response of forests to wildfire and logging, with the latter causing the conversion of conifer dominated

stands to deciduous stands. When designing ecologically based forest management systems managers have to understand and apply these results.

1.7 Summary

A review of the literature suggests that much is known about the role of fire in northern forests and how fire affects understory vegetation. Recovery of vascular vegetation after fire is from species that occupied the area before the fire and then recovered vegetatively or from remaining soil seed bank sources, with some migrant species invading the burned area. Over time, these understory vascular species decrease in abundance and size due to changes in the microclimate, mainly induced by canopy closure. This suggests that species in the northern forests could be adapted to recurrent fires and follow a successional pattern of initial floristics. In contrast, non-vascular species follow a pattern of facilitative relay floristics during succession, whereby one group of species replaces another as the severity of the micro-climate decreases and the habitat stabilizes.

The role of fire skips, which are patches that survive crown fires, in the ecology of subalpine forests is not understood. Skips themselves add to the biological, structural, landscape and spatial diversity of burned areas and could contribute migrant species to the initial recovery and succession of burned areas. The location of skips on the landscape seems dependent upon topography, which determines skip proximity to water bodies, fuel breaks and depressional areas.

As forestry companies begin to utilize ecologically based forest management practices, understanding the ecological role of fire skips becomes imperative. If skips themselves add to the biological and structural diversity of burned areas and contribute migrant species to the initial recovery and succession of burned areas, patches in cut-overs could play a similar ecological role. To accomplish this, the relationship between skip size to the biological diversity of the skips themselves and adjacent areas within the burned region needs to be better understood.

1.8 Objectives

The objectives of this study were to:

1. Classify and describe the understory plant communities of a burned area, associated fire skips, and adjacent unburned forest in a upper foothills - subalpine region of northwestern Alberta.
2. Evaluate the role of fire in the classification of the burned area, associated fire skips and adjacent unburned forest in a upper foothills - subalpine region of northwestern Alberta.
3. Discuss the possible implications that this fire skip research will have for future forest biology research and future forest management in the upper foothills - subalpine forest region.

1.9 References

- Acker, S.A, Zenner, E.K. and Emmingham, W.H. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. *Canadian Journal of Forest Research* 28: 749-758.
- Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. *Ecology* 41: 431-445.
- Anderson, R.C., Loucks, O.L. and Swain, A.M. 1968. Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. *Ecology* 50: 255-263.
- Andison, D.W. 2000. Landscape-level fire activity on foothills and mountain landscapes of Alberta. Foothills Model Forest, Alberta Foothills Disturbance Ecology Series, Report No. 2. Hinton, Alberta.
- Archibold, O.W. 1978. Buried viable propagules as a factor in post-fire regeneration in northern Saskatchewan. *Canadian Journal of Botany* 57: 54-58.
- Armour, C.D., Bunting, S.C. and Neuenschwander, L.F. 1984. Fire intensity effects on the understory in Ponderosa pine forests. *Journal of Range Management* 37: 44-49.
- Arno, S.F. 1980. Forest fire history in the Northern Rockies. *Forest Science* 98: 460-465.

- Arnott, J.T. and Beese, W.J. 1997. Alternatives to clearcutting in BC Coastal Montane forests. *The Forestry Chronicle* 73: 670-678.
- Baath, E., Frostegard, A., Pennanen, T. and Fritze, H. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous soils. *Soil Biology and Biochemistry* 27: 229-240.
- Barrett, S.W., Arno, S.F. and Key, C.H. 1991. Fire regimes of western larch - lodgepole pine forests in Glacier National Park, Montana. *Canadian Journal of Forest Research* 21: 1711-1720.
- Beckingham, J.D., Corns, I.G.W. and Archibald, J.H. 1996. *Field Guide to Ecosites of West-Central Alberta*. UBC Press. Vancouver, British Columbia.
- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* 72: 1980-1992.
- Bergeron, Y. and Dansereau, P. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *Journal of Vegetation Science* 4: 827-832.
- Bessie, W.C. and Johnson, E.A. 1995. The relative importance of fuels and weather on fire behaviour in subalpine forests. *Ecology* 76: 747-762.
- Black, R.A. and Bliss, L.C. 1978. Recovery sequence of *Picea mariana* - *Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Canadian Journal of Botany* 56: 2020-2030.
- Bondrup-Nielsen, S. 1995. Forestry and boreal forest: maintaining inherent landscape patterns. *Water, Air and Soil Pollution*. 82: 71-76.
- Bormann, B.T. and Sidle, R.C. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology* 78: 561-578.
- Brais, S., Camire C., Bergeron, Y. and Pare, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. *Forest Ecology and Management* 76: 181-189.
- Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist* 105: 467-478.

- Buckley, R. 1984. The role of fire: response to Snyder. *Oikos* 43: 405-406.
- Carleton, T.J., Jones, R.K. and Pierpont, G. 1985. The prediction of understory vegetation by environmental factors for the purpose of site classification in forestry: an example from northern Ontario using residual ordination analysis. *Canadian Journal of Forest Research* 15: 1099-1108.
- Carleton, T.J. and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey on the central Canadian boreal forest. *Ecoscience* 1: 141-152.
- Carleton, T.J. and Maycock, P.F. 1980. Vegetation of the boreal forests south of James Bay: non-centered component analysis of the vascular flora. *Ecology* 61: 1199-1212.
- Chapman, R.R. and Crow, G.E. 1981. Application of Raunkiaer's life form system to plant species survival after fire. *Bulletin of the Torrey Botanical Club*. 108: 472-478.
- Chrosciewicz, Z. 1986. Foliar moisture content variations of four coniferous tree species of central Alberta. *Canadian Journal of Forest Research* 16: 157-162.
- Collins, B.S., Dunne, K.P. and Pickett, S.T.A. 1985. Response of forest herbs to canopy gaps. In: *The ecology of natural disturbance and patch dynamics* (Eds.) Pickett, S.T.A. and White, P.S. Academic Press. Orlando, Florida. Pp. 218-234.
- Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144.
- Cumming, S.G., Burton, P.J. and Klinkenberg, B. 1996. Boreal mixedwood forests may have no "representative" areas: some implications for reserve design. *Ecography* 19: 162-180.
- DeGrandpre, L., Gagnon, D. and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. *Journal of Vegetation Science* 4: 803-810.
- Dix, R.L. and Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Canadian Journal of Botany* 49: 657-676.

- Dyrness, C.T., Van Cleve, K. and Levison, J.D. 1989. The effect of wildfire on soil chemistry in four forest fire types in interior Alaska. *Canadian Journal of Forest Research* 19: 1389-1396.
- Eberhart, K.E. and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17: 1207-1212.
- Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Flinn, M.A. and Wein, R.W. 1977. Depth of underground plant organs and theoretical survival during fire. *Canadian Journal of Botany* 55: 2550-2554.
- Foster, D.R. 1983. The history of and pattern of fire in the boreal forest of southeastern Labrador. *Canadian Journal of Botany* 61: 2459-2471.
- Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (Black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. *Journal of Ecology* 73: 517-534.
- Foster, D.R. and King, G.A. 1986. Vegetation Pattern and diversity in southeast. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. *Journal of Ecology* 74: 465-483.
- Fryer, G.I. and Johnson, E.A. 1988. Reconstructing fire behaviour and effects in a subalpine forest. *Journal of Applied Ecology* 25: 1063-1072.
- Gauthier, S., Leduc, A. and Bergeron, Y. 1996. Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. *Environmental Monitoring and Assessment* 39: 417-434.
- Granstrom, A. 1987. Seed viability of fourteen species during five years of storage in a forest soil. *Journal of Ecology* 75: 321-331.
- Greene, D.F. and Johnson, E.A. 2000. Tree recruitment from burn edges. *Canadian Journal of Forest Research* 30: 1264-1274.
- Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703-1715.
- Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70: 704-720.

- Halpern, C.B. and Franklin, J.F. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. *Journal of Vegetation Science* 1: 475-482.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3: 329-382.
- Heinselman, M.L. 1971. The natural role of fire in northern conifer forests. In: *Fire in the northern environment - a symposium*. (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 61-72.
- Hoehne, L.M. 1981. The groundlayer vegetation of forest islands in an urban-suburban matrix. In: *Forest island dynamics in man-dominated landscapes*. (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 41-54.
- Hornberg, G., Zackrisson, O., Segerstrom, U., Svensson, B.W., Ohlson, M. and Bradshaw, R.H.W. 1998. Boreal swamp forests - biodiversity "hotspots" in an impoverished forest landscape. *BioScience* 48: 795-802.
- Hunter, M.L. Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65: 115-120.
- Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. *Canadian Journal of Botany* 53: 2933-2941.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press. Cambridge, Great Britain.
- Keane, R.E., Ryan, K.C. and Running, S.W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with ecological process model FIRE-BGC. *Tree Physiology* 16: 319-331.
- Kutiel, P. and Naveh, Z. 1987. The effect of fire on nutrients in a pine forest soil. *Plant and Soil* 104: 269-274.
- Lack, D. 1969. The number of bird species on islands. *Bird Study* 16: 193-209.

- Levenson, J.B. 1981. Woodlots as biogeographic islands in outtheastern Wisconsin. In: Forest island dynamics in man-dominated landscapes. (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 13-39.
- Loope, L.L. and Gruell, G.E. 1973. The ecological role of fire in the Jackson Hole area, northwest Wyoming. *Quaternary Research* 3: 425-443.
- Martin, R.E., Miller, R.L. and Cushwa, C.T. 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56: 1441-1445.
- Matlack, G.R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. *Journal of Ecology* 82: 113-123.
- McGee, G.G., Leopold, D.J. and Nyland, R.D. 1995. Understory response to spring time prescribed fire in two New York transition oak forests. *Forest Ecology and Management* 76: 149-168.
- McLean, A. 1969. Fire resistance of forest species as influenced by root systems. *Journal of Range Management* 22: 120-122.
- Michalsky, S.J. 1987. Prescribed Crown Fire Effects on a Subalpine Bighorn Sheep Range at Ram Mountain in Alberta, Canada. M.Sc. Thesis. University of Alberta. Edmonton, Alberta.
- Moore, J.M. and Wein, R.W. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* 55: 2408-2412.
- Morneau, C. and Payette, S. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. *Canadian Journal of Botany* 67: 2770-2782.
- Mutch, R.W. 1970. Wildland fires and ecosystems-a hypothesis. *Ecology* 51: 1046-1051.
- Noble, M.G., DeBoer, L.K., Johnson, K.L., Coffin, B.A., Fellows, L.G. and Christensen, N.A. 1977. Quantitative relationships among some *Pinus banksiana* - *Picea mariana* forests subjected to wildfire and postlogging treatments. *Canadian Journal of Forest Research* 7: 368-377.
- North, M., Chen, J., Smith, G., Krakowiak, L. and Franklin, J. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. *Northwest Science* 70: 24-35.

- Pare, D., Bergeron, Y. and Camire, C. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. *Journal of Vegetation Science* 4: 811-818.
- Payette, S., Morneau, C., Sirois, L. and Despons, M. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70: 656-673.
- Pietikainen, J. and Fritze, H. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. *Soil Biology and Biochemistry* 27: 101-109.
- Pyne, S.J., Andrews, P.L. and Laven, R.D. 1996. *Introduction to Wildland Fire*. John Wiley and Sons. New York, New York.
- Quirk, W.A. and Sykes, D.J. 1971. White spruce stringers in a fire-patterned landscape in interior Alaska. In: *Fire in the northern environment - a symposium*. (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 179-197.
- Ranney, J.W., Bruner, M.C. and Levenson, J.B. 1981. The importance of edge in structure and dynamics of forest islands. In: *Forest island dynamics in man-dominated landscapes* (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 67-95.
- Rogeanu, M-P. 1996. *Understanding Age-Class Distributions in the Southern Canadian Rocky Mountains*. M.Sc. Thesis. University of Alberta. Edmonton, Alberta.
- Romme, W.H. and Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62: 319-326.
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service Research Paper INT-115.
- Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. *Canadian Journal of Botany* 39: 1007-1017.
- Rowe, J.S. and Scotter, G.W. 1973. Fire in the boreal forest. *Quaternary Research* 3: 444-464.

- Schaefer, J.A. 1993. Spatial patterns in taiga plant communities following fire. *Canadian Journal of Botany* 71: 1568-1573.
- Schimmel, J. and Granstrom, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77: 1436-1450.
- Shafi, M.I. and Yarranton, G.A. 1973. Vegetational heterogeneity during a secondary (postfire) succession. *Canadian Journal of Botany* 51: 73-90.
- Snyder, J.R. 1984. The role of fire: Mutch ado about nothing? *Oikos* 43: 404-405.
- Strauss, D., Bednar, L. and Mees, R. 1989. Do one percent of fires cause ninety-nine percent of the damage? *Forest Science* 35: 319-328.
- Strong W.L. and Leggat K.R. 1981. Ecoregions of Alberta. Alberta Energy and Natural Resources, ENR Technical Report Number T/4. Edmonton, Alberta.
- Swanson, F.J. and Franklin, J.F. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2: 262-274.
- Sylvester, T.W. and Wein, R.W. 1981. Fuel characteristics of arctic plant species and simulated plant community flammability by Rothermel's model. *Canadian Journal of Botany* 59: 898-907.
- Tande, G.F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany* 57: 1912-1931.
- Van Wagner, C.E. 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* 7: 23-34.
- Van Wagner, C.E. 1967. Seasonal variation in moisture content of eastern Canadian tree foliage and the possible effect on crown fires. Minister of Forestry and Rural Development, Forestry Branch, Departmental Publication No. 1204. Ottawa, Ontario.
- Van Wilgen, B.W., Higgins, K.B. and Bellstedt, D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone Fynbos shrublands of South Africa. *Journal of Ecology* 78: 210-222.
- Wein, R.W. and MacLean, D.A. (Eds.). 1983. The role of fire in northern circumpolar ecosystems. John Wiley and Sons. New York, New York.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *The Botanical Review* 45: 229-299.

- Woodard, P.M. 1977. Effects of Prescribed Burning on Two Different-Aged High-Elevation Plant Communities in Eastern Washington. Ph.D. Thesis. University of Washington. Seattle, Washington.
- Wright, H.A. and Bailey, A.W. 1982. Fire ecology United States and southern Canada. John Wiley and Sons. New York, New York.
- Wright, H.E. Jr. and Heinzelman, M.L. 1973. The ecological role of fire in natural conifer forests of western and northern America. *Quaternary Research* 3: 317-328.
- Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos* 29: 22-32
- Zasada, J.C. 1971. Natural regeneration of interior Alaska forests - seed, seedbed, and vegetative reproduction characteristics. In: *Fire in the northern environment - a symposium*. (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 231-246.

II. FIRE SKIPS AND UNDERSTORY PLANT DIVERSITY IN AN UPPER FOOTHILLS - SUBALPINE FOREST IN NORTHWESTERN ALBERTA

2.0 Introduction

Fire has been one of the primary natural disturbances in forests of the circumpolar north (Heinselman 1971, Rowe 1961, White 1979, Wright and Bailey 1982, Wein and Maclean 1983, Johnson 1992). Fire type, intensity, duration, severity and extent determine post-fire composition and succession of the flora and fauna (Heinselman 1971, Tande 1979, Foster 1983, Payette et al. 1989, Keane et al. 1996). Fire regimes are not consistent across the northern forests varying spatially and temporally among and within regions (Heinselman 1973, White 1979, Wright and Bailey 1982, Wein and Maclean 1983, Foster 1983, Payette et al. 1989, Rogeau 1996, Andison 2000). In subalpine areas across the interior northwest of North America, upland areas are subject to frequent and intense fires and are therefore dominated by even-aged stands of sub-climax lodgepole pine (*Pinus contorta* Loudon). Lowland areas are subjected to less intense fires, have higher soil moisture and therefore undergo more rapid succession resulting in domination by Englemann spruce (*Picea engelmannii* Parry ex Englem.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) stands. Rapid changes in topography or moisture can cause fire exclusion and therefore variable age class patterns across the landscape (Tande 1979, Arno 1980, Romme and Knight 1981, Fryer and Johnson 1988, Keane et al. 1996, Rogeau 1996, Andison 2000).

Most fires in Alberta are less than 200 ha in size, however, the 3% of fires of greater size are responsible for 95% of the total area burned (Eberhart and Woodard 1987, Strauss et al. 1989). Although these larger fires may have increased capacity for damage they are not homogeneous in composition. Rarely does all the vegetation within the main fire perimeter burn. Patches of vegetation are typically left within the larger burned area and can range in size from a clump of trees to tens of hectares (Eberhart and Woodard 1987). More fire skips of larger sizes are usually

found in larger fires because smaller fires might not be large enough, or burn long enough to encounter conditions leading to fire skip formation (Eberhart and Woodard 1987).

Hornberg et al. (1998) reviewed research from 13 boreal swamp forests in Sweden over a decade. The mean fire return interval was over 400 years compared to 50 to 180 year intervals for surrounding forests. Many swamp forests are true fire free refugia, having never been burned. Most refugia occur in low areas where risk of ignition by lightning is low. Continuous wet conditions promote reproduction and growth of hydrophilous species, which do not desiccate, lowering the risk of encroachment by ground fires from drier surrounding forests. Microhabitat variability within swamp forests creates an irregular fire pattern compared to surrounding forests. Quirk and Sykes (1971) found unburned patches of 200-year-old white spruce that survived several fire cycles surrounded by areas of 34-year-old white spruce. These stringers were found in depressions with increased soil moisture and a sudden change in micro-relief. Chrosiewicz (1986) found moisture content was highest in new foliage when lowest in old foliage. Van Wagner (1967) found trees with increased foliar moisture content produced less radiant heat, which could prevent the crowning of a fire. Thus, continual wet zones, sudden changes in topography and micro-relief and interruptions in the fuel bed continuity, such as bare rock and soil, may account for fire skip formation (Quirk and Sykes 1971, Heinzelman 1973, Rowe and Scotter 1973, Eberhart and Woodard 1987, Fryer and Johnson 1988, Bergeron 1991).

Fire effects on understory plant growth and reproduction are complex and not fully understood. Wright and Heinzelman (1973) suggest fire may selectively eliminate part of the understory plant community components, alter seedbeds by removing litter and humus, create areas of bare soil, trigger release of seeds and stimulate shrub and herb flowering and fruiting. This influences germination and survival of many forest species. Fire may also stimulate vegetative reproduction of many woody and herbaceous species when the overstory is reduced and sprouting from roots, root collars and lignotubers is common (McLean 1969, Chapman and Crow 1981). At the community level, fire temporarily reduces competition for moisture, nutrients and

light thereby selectively favoring some species. Fire frequency influences community composition and successional stage and controls overstory age for vegetation types experiencing crown fires.

Revegetation is principally from buried seed and/or underground plant parts within the burned area, or from seed transported after fire (Ahlgren 1960, Zasada 1971, Johnson 1975, Moore and Wein 1977). Severe fires eliminate seeds and root material from organic layers and recolonization occurs from reproductive material in mineral soil or migrant seed material. Less severe burns promote species whose propagules survive the fire in organic layers (Chapman and Crow 1981).

As succession continues, pre-burn understory communities become similar to post-burn communities, especially for vascular species (Black and Bliss 1978, Michalsky 1987, Halpern 1988, 1989, Morneau and Payette 1989, Halpern and Franklin 1990, Bergeron and Dansereau 1993, DeGrandpre et al. 1993). In a subalpine region of Alberta, Michalsky (1987) found most plants recovered after a prescribed burn, except for trees and shrubs. One-year post-fire and pre-fire species composition was similar with grass and sedge cover increasing after fire, and forb cover initially decreasing but recovering after one year.

Many researchers believe edges resulting from fires, harvesting or other disturbances can alter understory communities in forested areas (Hoehne 1981, Levenson, 1981, Ranney et al. 1981, Matlack 1994). Matlack (1994) found edge species primarily orient towards high light environmental gradients resulting in a distinct microclimate. This orientation was greatest immediately after removal of standing trees resulting in expanding herb, shrub and tree populations due to increased opportunities for vegetative propagation and seedling recruitment. Hoehne (1981), Levenson (1981) and Ranney et al. (1981) studied forested islands in agricultural and urban landscapes in southern Wisconsin. Levenson (1981) found species richness of these islands was a function of disturbance, increasing until islands reached approximately 2.3 ha and decreasing until islands reached 3.8 ha. Interiors of larger islands contained characteristic species of the original forests without many invasive and non-native species found in edge areas. Smaller islands functioned as edge communities without shade tolerant trees found in larger islands.

Ranney et al. (1981) found edge areas of islands were typically 15 m wide and structurally distinct from island interiors. Edge areas had richer tree species composition, with species intermediate to intolerant of shade, and increased tree basal area and density. Hoehne (1981) found greater understory diversity compared to the recent past due to invasion by weedy and exotic species from surrounding agricultural areas. Many native species decreased in frequency and abundance, or were eliminated from these islands due to invasions, continual disturbance and overall reduction in total available habitat.

Few studies focus on the understory plant communities of upper foothills and subalpine areas in northwestern Alberta and the ecological roles of fire skips in this area have not been studied. Thus, the objectives of this study were to classify and describe the understory plant communities and to determine the role of fire in the classification of a large burned area, its associated fire skips and adjacent unburned forest in an upper foothills - subalpine region of northwestern Alberta. This study is on a solitary fire, and therefore a case study of the possible implications fire skips have for post-burn plant communities.

2.1 Materials and Methods

2.1.1 Study Area

The study area was approximately 160 km southwest of Grande Prairie, Alberta (Sec. 25, Twp. 60, Rge. 13, W6) within the Forest Management Agreement Area of Weyerhaeuser Company Ltd. - Canada - Grande Prairie / Grande Cache Operations. It is dominated by coniferous forests and characterized by snowy cold winters and showery cool summers (558 to 752 growing degree days, 538 to 568 mm mean annual precipitation) (Beckingham et al. 1996).

The upper foothills region is located from 900 to 1500 m above sea level with lodgepole pine (*Pinus contorta* Loudon) stands dominating, but white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) considered the climax tree species. The subalpine natural region is located 1300 to 2000 m above sea level. In those areas with more precipitation, mixed Englemann spruce /

subalpine fir (*Picea englemannii* Parry ex Engelm. / *Abies lasiocarpa* (Hook.) Nutt.) stands dominate (Strong and Leggat 1981) and are considered the climax species, while on drier sites lodgepole pine is considered a seral species. Pure stands of Englemann spruce do not exist in these subalpine regions and stands are likely hybrids of Englemann and white spruce (Beckingham et al. 1996). The understory species between the natural regions is similar, but heathers (*Ericaceae* sp.) and certain shrubs, become more dominant in the subalpine (Beckingham et al. 1996).

The soils of lodgepole pine stands in the upper foothills region are characterized by a variety of parent materials formed into Eutric Brunisols (Strong and Leggat 1981). Other soils are Luvisols, Gleysols and Organics. Many Eutric Brunisols may be too xeric for invasion of spruce. In contrast, soils of the subalpine formed from morainal and colluvial materials into dominantly Brunisols and Regosols (National Soil Survey Committee of Canada 1987, Beckingham et al. 1996).

The study area fire (Provincial Fire Number DG2-013-82) started by lightning on June 18, 1982 and burned for 6 days before it was brought under control, then burned another 24 days before being extinguished. In 1982 dollars the suppression costs were \$587,325 and 77,726 cords of timber were consumed (Strickland 1995, Alberta Environment 2000). The study site is 1,138 ha in size and contains 46 fire skips ranging from 6.37 m² (6.37 x 10⁻⁴ ha) to 109,236 m² (10.92 ha). The majority of fire skips are less than 1 ha and only three fire skips are greater than 5 ha (Table 2.1). The skips do not follow a particular shape pattern (Figure 2.1). A digital map of the site provided by Weyerhaeuser Company Ltd. was analyzed using a Geographic Information System (GIS) to determine fire size, skip sizes and skip shapes (Figure 2.1).

2.1.2 Experimental Design

The fire skips within the burned area were divided into three size classes: Class 1 (>5 ha), Class 2 (1.5 to 5 ha) and Class 3 (<1.5 ha) (Figure 2.2). Three fire skips in Class 3 (18, 22, 23) and two in each of Class 1 (44, 46) and Class 2 (41, 43) were sampled along with the burned area and adjacent unburned forest (Table 2.1). An uneven number of fire skips were sampled due to accessibility limitations. Class 1

fire skips had a large core area and Class 2 skips had small core areas, both with visual edge effects; while Class 3 skips had no core areas and were completely edge affected. Edge effects were approximately one tree height in from the skip edge. 30 m was chosen as the maximum tree height because this height was greater than the tallest trees measured within and around the study area. Thus, Class 3 fire skips had diameters approximating two tree heights or less and all Class 3 fire skips were less than 40 m in width.

2.1.3 Treatments

Treatment areas were fire skip cores (treatment 1), unburned inside edges (treatment 2), outside burned edges immediately around each fire skip (treatment 3), unburned lodgepole pine forest (treatment 4), unburned Englemann spruce / white spruce hybrid forest (treatment 5) and the burned area (treatment 6) (Table 2.2). The fire, compared to the unburned surrounding forest, distinctly influenced these treatments. The burned area was directly and heavily influenced by the fire with total removal of overstory and understory plant species, and loss of soil organic matter. The fire marginally influenced fire skips by possible under-burning and resulting edge effects, but the overstory primarily remained intact (Figure 2.3). A skip edge was defined as the border between trees whose crowns had been destroyed or altered by the fire and were no longer alive and those trees whose canopy may have been affected by fire but were still alive (Figure 2.3). Riparian areas were distinct communities within fire skips thought to contribute to understory biological diversity of fire skips. Thus, they were sampled separately, but not considered a separate treatment. Burned riparian areas (treatment 7) were completely altered by the fire (Table 2.2). Riparian zones were defined as areas with permanent streams.

2.1.4 Field Measurements

Understory vegetation was assessed from early June to mid August 1998. Three line transects (samples) were placed through the middle of each skip (Tables 2.2 and 2.3), except the second largest skip, which had nine transects. In each fire skip a minimum 0.3% of the total area was sampled; 3% of Class 2 and 3 fire skips were sampled. Transects ran parallel and equidistant to each other across the face of the

slope of the skip. Classes 1 and 2 skip transects started and ended at least 30 m from the skip edge to eliminate edge effects; Class 3 skip transects were placed 5 m from the skip. In some Class 1 and 2 skips, core area transects were started up to 60 m in from the edge due to possible under-burning influencing understory vegetation.

In medium and large fire skips (treatments 2 and 3), a representative edge section was sampled. Topography rather than aspect determined species composition surrounding skip edges, therefore low lying wet and steep sloped areas were not sampled. Edge transects paralleled the skip edge and ran 2.5 m from the inside and outside edge of the skip. Two outside and inside paralleling edge transects were completed for Class 1 and 2 fire skips. Only outside edges of Class 3 fire skips were sampled because these skips were assumed to be completely edge affected due to their small size (Ranney et al. 1981) (Figure 2.3).

In unburned lodgepole pine areas (treatment 4), unburned Englemann spruce / white spruce hybrid areas (treatment 5) and burned areas (treatment 6) transects were placed randomly within the treatment and in random directions if possible (Figure 2.3). Where slopes were >35%, transects were placed across the slope face to reduce variability. Transect length varied from 60 to 150 m, and was usually limited because of changes in stand uniformity, topography or other physiographic features. Riparian transects were run parallel to stream edges.

Quadrats (subsamples) were systematically placed every 10 m along each transect (samples) (Table 2.2). 2.25 m² quadrats were used for shrub species, while 0.1 m² quadrats were nested within the lower right corner of the larger quadrats for grass forb, lichen and moss species. Quadrats were consistently placed on the north side of the transect, except for edge and riparian quadrats. Edge quadrats were placed facing the skip edge. Riparian quadrats were placed directly on the stream edge (0 m buffer), facing away from the stream into the surrounding vegetation.

Individual plants in the understory were identified to species if possible. Percent cover of species, foliage, bareground, rock, litter and coarse woody debris were recorded for each quadrat. Using species cover, species richness, diversity and evenness were calculated with the Shannon-Weiner Index (Kent and Coker 1992) for

all samples except edge transects where logistical constraints prevented cover data collection.

Overstory tree composition, diameter-at-breast-height (dbh), height, increment bores, organic matter thickness and percent slope were measured on a belt transect in the same location as the understory vegetation transects. The belt transect was 2 m wide, while length was 2.25 m multiplied by the number of quadrats per transect. A tree was measured if $\geq$ half of its diameter was within the transect. To ensure a representative sample of each skip, belt transects 1 and 3 were sampled starting at one end and belt transect 2 starting at the other end of the skip. In the second largest skip with nine transects each transect was sampled started at alternating ends. Since measurements of tree composition, dbh and height could not be completed within the burned area the number of standing trees and stumps were counted. Randomly along each transect a number of increment bores were taken from dominant overstory trees to determine overall stand age with a minimum of five cores from each transect. Incremental growth rings were counted in the field. Using height, dbh and tree species data from each transect tree density and tree volume (m^3) per ha were calculated. Tree volumes for pine and spruce were calculated using formulae from Alberta Energy and Natural Resources (1985). Subalpine fir volume calculations were completed using the spruce formulae. Stand age was calculated using the five oldest ages from each transect.

Organic matter depth was measured every 2 m along each belt transect as an estimate of fire severity. Depth was measured from the top of the organic layer (LFH layer) to the top of mineral soil, or from the top of the organic layer to the top of standing water beneath and averaged for each transect.

2.1.5 Data Analyses

Initially, mean species cover for an entire transect was calculated from each quadrat on it, creating 66 samples for analysis. Due to concerns about pseudo-replication all core and inside and outside edge transects were combined into single means for understory species cover data, resulting in 44 samples for analysis (Table 2.3).

Two-way indicator for species analysis (TWINSpan) (Hill et al. 1975, Hill 1979) was used to hierarchically divide these 44 samples into community types and find indicator species for each delineated community type. All default settings were used in the analysis, except number of pseudo-species cut levels (abundance) were changed from the standard five (0, 2, 5, 10 and 20) to eight (0, 0.25, 0.50, 1, 2, 5, 10 and 20) because average cover values for most of the 44 samples were below 2%, with many under 1% (Table 2.4).

Rare species were not down-weighted because mean cover values for many species were low (Table 2.4) and this study is attempting to account for entire understory plant species diversity not just dominant species. To determine if non-vascular and vascular plant species responded differently to treatments two other TWINSpan analyses were completed, with either vascular or non-vascular plant species used as indicator species. Burned riparian samples were not included in any TWINSpan analyses. More divisions were completed by TWINSpan than included in Figure 2.4, further separating many groupings. However, successive divisions were stopped when groupings contained less than 3 samples, as excessive divisions into very small and unrepresentative groupings were considered spurious and ecologically insignificant.

Further multivariate analysis of the 44 samples and their associated understory plant species cover values was completed using Canonical Correspondence Analysis (CANOCO, version 3.10) (ter Braak 1988, ter Braak 1990) (Table 2.3). An unconstrained (indirect) Detrended Correspondence Analysis (DCA) unimodal approach was more appropriate than the linear approach of Principal Components Analysis (PCA), because it provided more spread and more adequate sample groupings than PCA. Detrending was necessary because of the prominent arch effect in species groupings resulting when only a correspondence analysis (CA) was completed (ter Braak 1986). DCA was used to determine which of the 44 samples were more similar in species composition and which species were associated with each sample. The resulting DCA was compared with the TWINSpan groupings to determine if there were similarities in hierarchical classification and groupings of the DCA.

A further DCA ordination determined the extent treatments and external factors are responsible for the plant community. Logistical constraints prevented collection of external data from 11 edge transects. Therefore cover (vegetation, bareground, litter, wood), stand age, organic matter depth, average transect slope, tree density per ha, tree volume per ha, species richness, species diversity and species evenness were averaged for each of the remaining 33 samples and passively regressed with the previous DCA to attempt further interpretation of the ordination (Table 2.3). The nominal variables (treatments) of large core, medium core, small core, spruce, pine and burned were included to locate the center of these groupings.

To determine whether measured external factors were impacting resulting ordinations a DCA was completed with external factors run as a co-variate file. A Detrended Canonical Correspondence Analysis (DCCA) was compared with the DCA to determine the extent treatments and external factors are causing variability of species composition and sample groupings. A Canonical Correspondence Analysis (CCA) was completed with the forward regression option of CANOCO to determine variance in species composition explained by treatments and whether the variance explained the treatments were significant. Other parameters from this CCA used to interpret the ordination results were Intraset Correlations, Canonical Coefficients and T-values. Neither of the ordinations included riparian burned or riparian core samples.

To determine relationships between skip size and diversity, linear regressions of skip size versus fire skip species richness, species diversity and species evenness from core areas were completed using Microsoft Excel (version Excel 97 SR-2). A variety of similarity indices comparisons determined how similar plant communities were among treatments. The Euclidean Distance Dissimilarity Index was chosen as it uses all species in its comparisons and provides greater calculated values further indicating dissimilarities (Kent and Coker 1992). A value of zero indicates two communities are identical, while there is no upper limit on dissimilarity. Comparisons were made between fire skips of different sizes and fire skips were compared to surrounding lodgepole pine and Englemann spruce communities. Dissimilarity indices between core and edge areas of fire skips were compared with

the burned plant community to indirectly determine the extent of species association among treatments and sub-treatments. Dissimilarity indices were used to determine the possible ecological role of riparian areas after fire and their ability to recover from fire. Burned riparian areas were compared with riparian areas fire skip cores, while core area samples (without riparian areas) were compared to the burned plant community.

2.2. Results

2.2.1 TWINSpan Classification

Based on 149 understory plant species, TWINSpan divided the 44 samples into 6 community types (Figure 2.4). The dendrogram of this classification includes all transects and corresponding groupings, all indicator species used in the divisions ranked in their order of importance with their corresponding abundance level and eigenvalue for each division. An eigenvalue is an indication of the strength of the ordination; the higher the eigenvalue the greater the differences between those two TWINSpan groupings. Indicator species have been placed with the grouping they are positively associated with. Several commission and omission errors were found in the classification. An omission error is when a sample is not in a group where it was expected by treatment determinants. A commission error is when a sample has been placed in a group where it was not expected by treatment determinants. The 13 burn samples (BU) were separated from all other samples in the first division. The separation was associated with the largest eigenvalue (0.636), possibly indicating fire is the predominant factor responsible for sample separation. Bunchberry (*Cornus canadensis* L.), the indicator species, was negatively associated with the burned grouping.

The Englemann spruce (ES) samples separated into a distinct group. One of the Englemann spruce samples was associated with a commission and an omission error. This grouping contained the large skip 2 core sample transects. Indicator species were glow moss (*Aulacomium palustre* Hedw.), cloud berry (*Rubus chamaemorus* L.) and bishop's-cap (*Mitella nuda* L.). The eight lodgepole pine samples separated into a distinct group (LP). Common leafy moss (*Plagiomnium*

medium (B.S.G.) Kopp), awned haircap moss (*Polytrichum piliferum* Hedw.) and white-flowered rhododendron (*Rhododendron albiflorum* Hook.) were negatively associated with the pine grouping.

The core samples of the large and medium skips separated as a distinct group (LMC) with an omission error. The associated inside and outside edge areas separated as distinct groups (LSE and MSE) with omission errors. Indicator species were fireweed (*Epilobium angustifolium* L.) for the LSE grouping and black twinberry (*Lonicera involucrata* (Richards.) Banks) for the MSE community type. The small core samples and their associated outside edge transects fell into three different groupings. Small skip 1 samples were placed in the Englemann spruce community while small skip 2 samples were placed in the lodgepole pine grouping creating several commission and omission errors. Only small skip 3 samples were grouped with other core samples from medium and large skips. However, the outside edge transect of small skip 3 could be considered a commission error.

The large and medium edge area groupings separated out most closely to the fire skip core grouping and most closely to the burned area. The Englemann spruce grouping separated out furthest from the burned groupings. The lodgepole pine grouping separated out between the Englemann spruce grouping and the large and medium core and edge groupings.

TWINSpan results for non-vascular species as indicators were similar to the results for the vascular species as indicators. These results were almost identical to the original all species as indicators results. Indicator species included in the separate vascular and non-vascular TWINSpan results were broom moss (*Dicranum scoparium* Hedw.), wavy dicranum (*Dicranum undulatum* Brid.), lungwort (*Lobaria pulmonaria* (L.) Hoffm.), meadow horsetail (*Equisetum pratense* Ehrh.), Labrador tea (*Ledum groenlandicum* Oeder), bog cranberry (*Vaccinium vitis-idaea* L.) and heart-leaved arnica (*Arnica cordifolia* Hook.).

2.2.2 Summary Table

Table 2.5 summarizes canopy cover for 149 species and various external factors for each of the 6 community types. Some species appear to have 0% canopy cover; this occurs when canopy cover is less than 2 decimal places. Most cover values for species of the 6 community types were less than 5%, with many species having cover values >1% (Table 2.5). Some species were found within all 6 community type groupings while others had very low values for only one or two of the groupings. A list of common and Latin names is provided in Table 2.10. Very few species have higher than average cover values for particular groupings. However, of the forb species, bunchberry (*C. canadensis* L.), twinflower (*Linnea borealis* L.), five-leaved bramble (*Rubus pedatus* J.E. Smith), sweet coltsfoot (*Petasites frigidus* L.) and wood horsetail (*Equisetum sylvaticum* L.) are only found in unburned plant community types. Purple-leaved willowherb (*Epilobium ciliatum* Raf.), arctic daisy (*Erigeron humilus* Grah.), arrow leaved groundsel (*Senecio triangularis* Hook.) and false solomon's seal (*Smilicina racemosa* (L.) Desf.) are associated with the burned grouping. Fireweed (*E. angustifolium* L.) and Nootka lupine (*Lupinus nootkatensis* Donn ex Simms) were associated with the lodgepole pine community and the large and medium edge communities. One-sided wintergreen (*Orthelia secunda* (L.) House) and meadow horsetail (*E. pratense* Ehrh.) were associated with Englemann spruce groupings. Most other forb species had low cover values associated with only one or two community types.

Most grass species had very low cover especially in the unburned community types. However, marsh reed grass (*Calamagrostis canadensis* (Michx.) Beauv.) was exclusively associated with the unburned community types. In contrast, northern reed grass (*Calamagrostis inexpansa* A. Gray) and mountain hairgrass (*Deschampsia atropurpurea* (Wahl.) Scheele) had much higher cover in the burned grouping compared to any other. Bristle-stalked sedge (*Carex leptalea* Wahlenb.) was exclusively found in the Englemann spruce community type.

Bog birch (*Betula glandulosa* Michx.), red honeysuckle (*Lonicera dioica* L.), black twinberry (*L. involucrata* (Richards.) Banks), northern black currant (*Ribes hudsonianum* Richards.), Drummond's willow (*Salix drummondiana* Barr. ex Hook.)

and Sitka willow (*Salix sitchensis* Sanson ex Bong.) all had higher cover with burned community type. Crowberries (*Empetrum nigrum* L.), Labrador tea (*L. groenlandicum* Oeder) and prickly rose (*Rosa acicularis* Lindl.) cover were higher with lodgepole pine communities. Black huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) were associated with most community types except burned areas. Beaked willow (*Salix bebbiana* Sarg.) and Pacific willow (*Salix lucida* ssp. *lassiandra* Benth.) had higher cover for Englemann spruce community types. White-flowered rhododendron (*R. albiflorum* Hook.) had high cover in all three skip groupings but lower values in the burned grouping and especially the Englemann spruce grouping.

Groupings of moss and lichen species were either associated with the burned or unburned community types, unlike many vascular species, which were found in both. Mosses (common leafy liverwort (*Barbilophozia lycopoides* (Wallr.) Loeske), broom moss (*D. scoparium* Hedw.), stair-step moss (*Hylocomium splendens* (Hedw.) B.S.G.), stiff club-moss (*Lycopodium annotinum* L.), Schreber's moss (*Pleurozium schreberi* (Brid.) Mitt.), knight's plume (*Ptilium crista-castrensis* (Hedw.) De Not.) and poor-fen sphagnum (*Sphagnum angustifolium* (Russ.) Tolf.) and lichens (frog pelt (*Peltigera neopolydactyla* (Gyel.) Gyel.) and club lichens (*Cladonia* sp.)) were associated with non-burned community types, especially the Englemann spruce and core community types. Reindeer (*Cladina* sp.) and club lichens were most strongly associated with lodgepole pine groupings. *Brachythecium* species, and *Polytrichum* species were primarily associated with the burned grouping, but especially slender hair-cap (*Polytrichum strictum* Brid.). No lichen species had high cover.

The burned community type had the highest bareground, total species cover and species evenness. Litter cover was higher in unburned compared to burned community groupings and highest in lodgepole pine and edge community groupings. Fallen wood cover was highest in the large and medium edge community groupings. Species richness was highest in Englemann spruce and large skip edge groupings, but surprisingly lowest in the medium skip edge grouping. However, the Shannon-Weiner Diversity Index was highest for the large skip edge community grouping.

while highest evenness values were found in the large skip and the medium skip edge groupings (Table 2.5).

2.2.3 Ordinations

The initial DCA, using only canopy cover of all species of the 44 samples, produced eigenvalues of 0.864 for axis 1 and 0.251 for axis 2, which accounted for 25.0% and 7.3% of the variation in species composition, respectively (Figure 2.5). The length of the first axis was 4.559 and the second axis was 2.379. According to ter Braak (1988), eigenvalues reveal the significance of each axis in accounting for species variation, indicating the first axis accounted for much of the species variation. The eigenvalues for axes 3 and 4 were 0.141 and 0.087 and only accounted for 4.1% and 2.5% of the variation in species composition, respectively. Thus, the ordinations of these axes were not included.

The greatest separation of the sites occurred along the first axis, which separated burned from unburned sites (Figure 2.5). Separation along the second axis was weaker, which was also indicated by the lower accountability of the second axis for variability in species composition. The lodgepole pine sites were widely separated from the Englemann spruce sites on the second axis. In between these groupings were the sites associated with each of the skips. Using the centroids as focal points for the center of each of the treatment types allowed the sites to be grouped.

The DCA of the 33 sites passively analyzed with the external factors (Figure 2.6) was similar to the DCA of all 44 sites (Figure 2.5). The first axis had an eigenvalue of 0.883 and the second axis had one of 0.321, with each axis accounting for 28.7 and 10.4% of the variation, respectively. The length of axis one was 5.038 while that of axis two was 2.426. Using centroids of the treatment types, in the first ordination, of the first axis, the burned sites were grouped separately from all unburned sites, with the remaining sites vertically separated again along the second axis. In general, lodgepole pine sites were separated furthest from the spruce sites with the core areas of the small, medium and large skips in between these two.

A passively analysed external factor is more strongly related with a species or site when the line representing that external is in the same direction as those species or sites. The longer the line representing an external factor the stronger the external factor is correlated to those particular sites or species (ter Braak, 1988, 1990). The external factors most closely associated with burned sites were bareground, total canopy cover, rock and species evenness. Wood cover and average slope of each transect were not strongly correlated with any of the sites. Litter was the only factor most closely associated with the pine grouping. Stand age, species diversity, species richness and organic matter depth were most closely associated with the Englemann spruce and core groupings. Of these external factors, organic matter depth and species richness were oppositely correlated with the burned areas.

The species most closely associated with the burned samples were shrubs and grasses. Of the remaining samples, a particular understory compliment was associated with each of the groupings. For example, *Sphagnum* sp. were associated with the Englemann spruce grouping while another compliment of mosses were associated with the lodgepole pine grouping. Most species associated with the Englemann spruce grouping were either mosses or low growing herbs and shrubs. Species associated with the various skip groupings were not as strong. This trend was also found in an analysis of the summary table of the TWINSPLAN groupings (Table 2.5). Species were only plotted if 35% of their variation was explained by a CA ordination.

A comparison of the original DCA and a DCCA revealed no significant differences between the two. In addition, the CCA with the external factors ran as covariates were similar to the both the DCA and the external factor DCA. The CCA was still similar to both DCAs when the independent covariates of slope and organic matter depth were used in the CCA (rather than all external factors). This indicates that treatments rather than external factors were the primary influences on variation in the understory plant community.

The results from the forward selection function of the CCA when the ordination centroids are used as treatments indicates that burning is the primary factor that explains the species variance in the understory plant community (57%) (Table 2.6).

Spruce, pine and small core treatments were also significant (at $P \leq 0.01$) in explaining the variance in community composition, but each explained much less of the variation compared to the burning treatment. Intraset correlations relate the treatments themselves to the axes while canonical coefficients are derived from the regressions of sample scores (Jongman et al. 1987, ter Braak 1988). An analysis of the canonical coefficients reveals that along the first axis burning is the most important treatment in explaining the variation in species composition. In contrast, for the second axis, the spruce, pine and large core treatments are most important in explaining variation in plant community composition. As expected an interpretation of the intraset correlation results reveal that the burned treatment is highly correlated with the first axis, while all other treatments are negatively correlated with the first axis. An interpretation of the intraset correlations for the second axis reveals the strong correlation and the large core and spruce treatments to the axis and a strong negative correlation for the pine treatment. Both medium and small core treatments are negatively correlated with the second axis while the burn treatment explains little of the variation along the second axis (Table 2.6).

2.2.4 External Factor Summary

A summary of external factors for each of the treatments confirms the results of the second ordination (Table 2.7). Both burned treatments had increased bareground while the burned riparian treatment had very high litter cover and less bareground. Increased amounts of fallen wood were associated with large skips and the burned area. Although the edge transects were not included in the sample and sub-sample summary table (Table 2.2), observations indicated the edge areas around skip of all sizes contained large amounts of fallen wood from burned trees. The large skips had the greatest species richness, along with Englemann spruce and burned treatments. The Shannon-Weiner Diversity Index results were similar, but the burned riparian area had the greatest diversity. As expected the greatest organic matter depths were associated with the skips and unburned areas and the greatest average slope was associated with the largest skips. Tree volumes were greatest for the Englemann spruce treatment and on average lower for the smaller skips. However, tree

densities were highest in the skips and burned area. The tree density for the burned area may be overestimated as burned stumps were used to estimate density.

2.2.5 Similarity Analysis

A review of the Euclidean Distance Dissimilarity Indices (Table 2.8) reveals that the understory plant community of the largest skips (Class 1) was most similar to that of the surrounding Englemann spruce forest. Both medium and small skips were more similar to the lodgepole pine community than the Englemann spruce community. When compared to both TWINSPLAN and ordination results, the similarity indices indicate Englemann spruce and lodgepole pine communities were very dissimilar and more similar to core communities of the fire skips (Table 2.8). In comparing skips themselves, the large and medium core understory plant communities were most similar with large and medium skips about equal in similarity to the small skips (Table 2.8).

A comparison of the three sizes of skip core areas, their respective edge transects and the burned area reveals interesting results. The edges of the large transects were more similar to their core area than the medium and small skips were to either of their edges. The most similar communities were inside and outside edge transects of the medium and large skips. The outside communities were more similar to the burned area than either core or inside edge communities (Table 2.9).

2.2.6 Diversity Size Relationship

In the three linear regressions completed, only the species richness versus skip size relationship was significant at a 95% confidence interval, with an R^2 of 0.82 (Figure 2.7). However, a linear relationship (positive for diversity and negative for evenness) does appear and the P-values were very close to significant at $\alpha = 0.05$ (Figures 2.8 and 2.9). Linear regressions were adequate for richness, diversity and evenness as most of the residuals were less or very close to or less than two for the seven data points used.

2.2.7 Riparian Areas

The riparian areas associated with large skip 1, large skip 2 and medium skip 3 contributed to the species diversity of these areas. The number of species contributed by the riparian areas for large skip 1 was 33, 20 species for large skip 2 and 38 species for medium skip 2, which could be considered significant. The riparian areas (burned and non-burned) were more similar than the non-riparian areas (burned and non-burned) (Table 2.8).

2.3 Discussion

2.3.1 Multivariate Analysis

Results of the TWINSpan groupings, DCA ordinations and CCA forward selection confirm the hypothesis that fire can be considered one of the primary factors determining composition of this upper foothills - subalpine understory plant community (Rowe 1961, Heinzelman 1971, White 1979, Wright and Bailey 1982, Wein and Maclean 1983). This must be considered within the context that individual fires vary considerably from one another, but each fire varies spatially and temporally due to external factors such as weather and to internal factors such as topography, foliar moisture content and other abiotic and biotic factors.

In most northern forests a flush of grass species appears after a fire, associated with increased cover of sun herbs and other light tolerant species, and a decrease in light sensitive species (shade herbs). This occurs as the amount and quality of light entering these areas change with removal of the overstory canopy (Black and Bliss 1978, Armour et al. 1984, Collins et al. 1985). Many after fire dominant plant species reproduce from underground parts (lignotubers, rhizomes) or seeds that were deep enough in the soil to survive the fire or entered the burned area as early successional migrants from surrounding plant communities (McLean 1969, Johnson, 1975, Moore and Wein 1977, Flinn and Wein 1977, Archibold 1978, Schaeffer 1993, Schimmel and Granstrom 1996). Many of these species have low cover in surrounding communities, indicating they may require fire for release, and may require or prefer the changed abiotic and biotic conditions the fire provides.

Species dominating after a fire are proficient at utilizing the change of nutrients (usually an increase of Ca, Mg and K and a decrease of N and P), the bareground available after the fire or even the heat from the fire to initiate germination, allowing them to dominate early in succession (Martin et al. 1975, Archibold 1978, Collins et al. 1985, Dyrness et al. 1989, Kutiel and Naveh 1987, Brais et al. 1995). Other researchers also found the more severely burned the site the longer it takes the plant community to return to pre-disturbance cover and abundance (Halpern 1988, 1989, Halpern and Franklin 1990).

Some of the TWINSpan indicator species reflect the species responses to fire reported by these researchers. Bunchberry (*C. canadensis* L.), a low growing herb, is classified as moderately susceptible to fire. Its rhizomes can survive severe fires if located in mineral soil rather than the LFH layer. After fire, it resprouts from rhizomes remaining in the soil, rather than germinating from seed and usually will remain at a site after fire. However at this site, the fire was quite severe removing most of the LFH layer and removing bunchberry from the burned area (Morris 1958, Fischer and Clayton, 1983). Cloudberry (*R. chamaemorus* L.) is often found in areas with deep organic layers, like the Englemann spruce community. Like bunchberry, cloudberry reproduces by rhizomes and therefore is susceptible to fire (Rapp et al. 1993). In contrast, fireweed (*E. angustifolium* L.) the indicator species for the edge community, is found in disturbed areas, such as those affected by fire, where the canopy has been opened. After fire, it can quickly dominate a site due to prolific wind dispersed seed and spreading rhizomes located deeper in the mineral soil and utilization of increased light (Fenton et al. 1984).

The responses to fire of the understory plant communities in this case study were similar to the responses noted by other researchers. The TWINSpan results for the vascular and non-vasculars as indicators were also similar, however, the response of the two communities to the fire was divergent. Many cover values for vascular plant species were extremely low so finding trends was difficult. However, none of the vascular species was endemic to the community types developed by TWINSpan, or the groupings developed by the DCA ordination. Not all understory species were found within all community types or ordination groupings, but most were found in

more than one community type at similar cover values. Though not explicitly tested in this study, this may indicate that vascular plant species succession is following the initial floristics model (Egler 1954) and inhibition and tolerance models (Connell and Slatyer 1977). This pattern, whereby most vascular plant species are included throughout succession, with the majority of changes being in abundance and cover, is common in other northern forest areas (Black and Bliss 1978, Carleton and Maycock 1980, Armour et al. 1984, McGee et al. 1995). In addition, as with other northern forest areas, there was an increase in grass cover and certain shrubs, with these species utilizing the modified abiotic and biotic conditions in the burned and edge areas.

In contrast, many non-vascular species were eliminated from the burned community type, as several cm of LFH layer were eliminated in the fire and many non-vascular species are sensitive to disturbances of this type. Distinct non-vascular plant species communities were found in the different TWINSPAN community types and the DCA ordination groupings, or had appreciably greater cover values in one community type. Therefore, though not explicitly tested, the relay floristics (Egler 1954) and the facilitation model (Connell and Slatyer 1977) may be the appropriate successional models for non-vascular plant species at this site. This assumption is further implied by increase in cover of *Cladina* and *Cladonia* species for the lodgepole pine community grouping and the domination by stair-step moss, Schreber's moss and knight's plume in the Englemann spruce community and fire skip core community groupings.

These results may indicate that groupings of non-vascular plant species replace one another in different community types as succession continues. After canopy closure, with ameliorated environmental conditions, non-vascular plant species dominate as they are less sensitive to low light and nutrient conditions. Canopy closure also increases soil moisture and soil water holding capacity further favouring development of a non-vascular dominated understory (Black and Bliss 1978, Foster 1985, Mournéau and Payette 1989). These results merely indicate different non-vascular plant species (or species groupings) have different environmental tolerances to environmental conditions within each community type / grouping.

The resulting different community types or treatments used in this study may reflect a time since fire successional pattern, if age since fire of the overstory dominants is used as an indicator of stand age. If this is assumed the burned treatment represents the earliest stage of succession and the Englemann spruce and largest skips treatment (Class 1) represent the last stages of succession, with small and medium fire skip (Class 2 and 3) treatments and the lodgepole pine treatment in between. In addition, the TWINSpan groupings do contain some commission and omission errors compared to our treatments using overstory tree composition or skip size as treatment determinants. Only the burned communities separated out in TWINSpan community types without errors, or without overlap in the DCA ordinations.

More important than succession may be the fire skip community groupings falling between Englemann spruce and pine communities in the DCA ordinations. Therefore, this may indicate that fire skips represent distinct communities on this site, especially the larger Class 1 and 2 skips. As the average age for the larger skips would indicate, they have survived one or even two previous crown fires in the region. Moreover, considering that the overstory of the Englemann spruce community is similar to that of the large and medium skips and their age similarity, it is anticipated that the DCA analysis of these treatments placed them appropriately closer to the Englemann spruce treatment. The Intraset Correlations also indicated that large core treatments and Englemann spruce treatments are correlated with the second axis while all other treatments are negatively correlated with the second axis, especially the lodgepole pine treatment. In relative terms the Canonical Coefficients indicate that the lodgepole pine and spruce treatments are more important in explaining the variance in community composition along the second axis.

Further similarity of the Englemann spruce communities and the large and medium skips is indicated by all three community types containing many later-successional non-vascular plant species, deep organic layers, fallen decaying logs, similar tree densities, similar tree volumes and similar average tree ages (Table 2.7). This has created a highly diverse community with low evenness due to the dominance of

feather moss species. They both contain a high percentage of subalpine fir in the understory and overstory and a higher percentage of fire sensitive vascular species such as bunchberry. Though they may have similar environmental conditions, they did not group together in the TWINSpan groupings, only in the ordinations. These results may indicate the Englemann spruce community is the source for the largest skips on the site.

The small skip 3 samples separating out in a TWINSpan grouping with the large and medium skip core samples may indicate that smaller skips are not as unique from larger skips as anticipated. This may be further indicated by the closeness in age of the small skips to the burned area and not having the edge areas of the small skips separate out in the TWINSpan groupings unlike the medium and large skips, which edge samples which formed their own groupings. Small skips may have been completely altered by light oriented edge effects as they were less than one tree height in width with no core areas. This may result in a change in their species compositions and further limit their ability to separate out with the large and medium skip cores in any TWINSpan analysis. However, this is not revealed in the summary data.

Both the large and medium skip edge communities (including inside and outside transects) separating as community types in TWINSpan, furthers the hypothesis that larger fire skips could be considered distinct plant communities at this site. In the ordinations these samples separated within the large and medium groupings delineated. These community types possessed a marked increase in grass and shrub cover especially in the outside edge samples. As the inside and outside edge samples for the medium and large skip separated together it is a possible indication of species migrations from the inside edge to the outside edge and vice versa, or merely that these areas are correlated due to their proximity (spatial auto correlation). However, it may be an indication that skips, especially larger ones, may act as a source for plant species as succession in the burned area continues. This is further confirmed with the dissimilarity index results.

2.3.2 Similarity Analysis

The Euclidian Distance Dissimilarity Index results further the argument that the plant communities of the largest skips (Class 1 and 2) most resemble those of the Englemann spruce areas at this site. However, medium and large skips are just as similar to one another. Moreover, the dissimilarity index results combined with similar abiotic and biotic conditions within these areas may indicate the low-lying Englemann spruce areas may be the source for the larger skips at this site. However, skips had greater average slopes possibly indicating only those Englemann spruce areas where there are distinct topographic changes escape fires. Why medium and small skips are more similar to the lodgepole pine communities is unknown. A comparison of skips reveals large and medium skips are more similar to each other than either is to smaller skips.

At this site larger (>1.5 ha in size) fire skips are not randomly placed on the landscape but are distinct communities protected from fire due to proximity of riparian areas and changes in topography that limit entry of crown fires. Most larger skips have greater average slope compared to the other communities, contained small streams and were located next to larger creeks. Smaller skips, which from field notes, were only found in low lying areas with subtly different topographies (less average slope as well) compared to their surroundings may then be more randomly placed on the landscape at this site. Further evidence for the non-random placement of large skip theory could be that the average ages for the large and medium skips are nearly twice that of the burned area and one tree in the largest skip was 284 years old. In contrast, the average age for smaller skips was close to that of the burned area at this site.

The Euclidean Distance Dissimilarity Index results for the core, edge and burned areas indicate minimal understory plant species movement between communities. Minimal species movement may be due to a continuous environmental gradient from the burned upland to the lowland skip areas. The continuous environmental gradient could be due to differences in composition and amount of light between the various communities. This post-fire gradient could be more responsible for variation in understory plant community composition of the treatments areas than any direct

effects from fire. These results support those of Matlack (1994) who found edge species orient to light-oriented environmental gradients, such as litter, moisture and temperature. The microclimate afforded by this gradient is greatest after removal of standing trees and lasts until the surrounding canopy can recover. The outside edges of the skips were completely affected by fire, including organic matter and canopy removal. Therefore it was expected that outside edges would be more similar to burned areas than inside edges. The similarity of inside and outside edge areas could indicate species movement between these areas is occurring or that these areas are merely spatially auto-correlated. The uniqueness of the edge areas of skips contributes to the possible consideration of the larger skips (cores and edge areas) as distinct plant communities on the landscape.

2.3.3 Diversity Size Relationship

The relationship of skip size to skip diversity for this site was confirmed with linear regression analysis. Lack (1969) and Brown (1971) found larger islands had greater habitat niches and therefore increased species richness. The core areas of the larger fire skips were not under-burnt by the 1982 fire, have not been altered by edge effects and have survived several fire cycles as indicated by their age, resulting in greater overall habitat stability. Therefore, the larger size of the Class 1 and 2 skips compared to smaller skips should result in a greater number of habitat niches. Increased habitation niches combined with the increased habitat stability of the larger skips (longer fire free interval) could result in a greater total number of plant species in these skips. The variable topography, riparian areas and fallen and decaying logs in larger size classes increase the biological and structural diversity of larger skips further increasing number of habitat niches and therefore species diversity. These factors may also be responsible for the increased species richness in the Englemann spruce areas. However, both Class 1 and 2 skips and Englemann spruce treatments have low species evenness due to dominance of non-vascular species.

These results are similar to those of Hornberg et al. (1998), who found fire free refugia contained higher species diversity compared to the surrounding forest, especially non-vascular species, and similar to the skips examined here, did not

contain any endemic species. Increased diversity in these swamp forests was due to increased habitat niches from downed wood, the presence of both upland and low lying areas, and from greater stability due to long fire-free intervals. These results further the argument that larger fire skips represent distinct communities at this site in the upper foothills – subalpine forest region. In contrast to Levenson et al. (1981) our small size Class 3 areas were not dominated by invasive plant species and were similar in species composition to the surrounding pine forests. In further contrast, larger skips had greater not lower diversity.

2.3.4 Riparian Areas

At this site, riparian areas may be more successful at recovering after a fire than upland burned areas, as well as contributing species to the richness of burned areas and larger skips. Burned riparian areas had less bareground, increased litter and higher diversity, all of which indicate that riparian areas may recover faster from fire. In this sense, burned riparian areas may be considered fast recovering communities that provide increased overall biological and structural diversity to the burned treatment.

2.3.5 Implications for Forest Management and Future Research

Recently, the forest industry has advocated ecologically-based forest management practices in response to criticism from the public and provincial forestry departments. These practices are designed to mimic natural disturbances and inherent landscape patterns, such as windfall and insect outbreaks, but especially fire at the landscape level (Swanson and Franklin 1992, Bondrup-Nielsen 1995, Hunter 1993). Green tree retention and patch retention harvesting systems are supplied as ecologically-based forest management practices to follow at the stand level (Arnott and Beese 1997). Biotic structures, such as standing trees, fire skips and snags, are acknowledged to play a role in the persistence and recovery of ecosystems after a disturbance such as fire (Swanson and Franklin 1992, Arnott and Beese 1997, Acker et al. 1998).

Thus, if skips larger than 1.5 ha (core samples and edge samples included) at this site seem to have the capability to survive several fire cycles they could be selected for patches in clear cuts by forest planners. Especially, if they seem to correlate to surrounding forest types, such as larger skips to Englemann spruce areas at this site. However, further research on other fires in other forest types is required to determine if larger patches have consistently greater species diversity and richness and are persistent on the landscape through several fire cycles. More research will also be required to determine the location of possible skip areas within clear cuts as they seem to be located in areas with changes in local topography and proximal to riparian areas. Subsurface hydrology of fire skips should also be researched to determine if increased subsoil moisture may factor into the formation of fire skips.

Research will be required to determine the optimum number of patches of various sizes to not only reflects landscape patterns but to ensure diversity of species contained within these areas remains on the landscape. Further research will be required at fires of similar ecology, but of different ages to determine if fire skips act as species storehouses and supply plant species to burned areas as succession continues. However, if further research indicates that these areas are not unique, are randomly located and do not contain endemic species, the selection and placement of patches in clear cuts is not as imperative.

2.4 Conclusions

In this case study, the classification and description of the understory plant communities of a burned area, associated fire skips and adjacent unburned forest indicate that fire could be considered one of the primary factors in determining understory plant species composition. The classification and further analysis indicate that larger fire skips (>1.5 ha) may not be located randomly on the landscape at this site as they have survived several fire cycles. Larger skips (including core areas, edge areas and riparian areas) could represent unique communities at this site due to their structural and biological diversity.

2.5 References

- Acker, S.A, Zenner, E.K. and Emmingham, W.H. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implication for green tree retention. *Canadian Journal of Forest Research* 28: 749-758.
- Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. *Ecology* 41: 431-445.
- Alberta Energy and Natural Resources. 1985. Alberta Phase 3 inventory: single tree volume tables volume sampling region 5. Alberta Forest Service, Resource Evaluation and Planning Division, ENR Report No. Dept. 86G. Edmonton, Alberta.
- Alberta Environment. 2000. 1981 and 1982 historical fire data. Provincial Forest Fire Centre, Forest Protection Division, Land and Forest Service. ftp://ftp.env.gov.ab.ca/jfw/Fires1981_82.dbf.
- Andison, D.W. 2000. Landscape-level fire activity on foothills and mountain landscapes of Alberta. Foothills Model Forest, Alberta Foothills Disturbance Ecology Series, Report No. 2. Hinton, Alberta.
- Archibold, O.W. 1978. Buried viable propagules as a factor in post-fire regeneration in northern Saskatchewan. *Canadian Journal of Botany* 57: 54-58.
- Arno, S.F. 1980. Forest fire history in the Northern Rockies. *Forest Science* 98: 460-465.
- Arnott, J.T. and Beese, W.J. 1997. Alternatives to clearcutting in BC Coastal Montane forests. *The Forestry Chronicle* 73: 670-678.
- Armour, C.D., Bunting, S.C. and Neuenschwander, L. F. 1984. Fire intensity effects on the understory in Ponderosa pine forests. *Journal of Range Management* 37: 44-49.
- Beckingham, J.D., Corns, I.G.W. and Archibald, J.H. 1996. Field Guide to Ecosites of West-Central Alberta. UBC Press. Vancouver, British Columbia.
- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* 72: 1980-1992.
- Bergeron, Y. and Dansereau, P. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *Journal of Vegetation Science* 4: 827-832.

- Black, R.A. and Bliss, L.C. 1978. Recovery sequence of *Picea mariana* - *Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. Canadian Journal of Botany 56: 2020-2030.
- Bondrup-Nielsen, S. 1995. Forestry and boreal forest: maintaining inherent landscape patterns. Water, Air and Soil Pollution. 82: 71-76.
- Brais, S., Camire C., Bergeron, Y. and Pare, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. Forest Ecology and Management 76: 181-189.
- Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist 105: 467-478.
- Carleton, T.J. and Maycock, P.F. 1980. Vegetation of the boreal forests south of James Bay: non-centered component analysis of the vascular flora. Ecology 61: 1199-1212.
- Chapman, R.R. and Crow, G.E. 1981. Application of Raunkiaer's life form system to plant species survival after fire. Bulletin of the Torrey Botanical Club. 108: 472-478.
- Chrosciewicz, Z. 1986. Foliar moisture content variations of four coniferous tree species of central Alberta. Canadian Journal of Forest Research 16: 157-162.
- Collins, B.S., Dunne, K.P. and Pickett, S.T.A. 1985. Response of forest herbs to canopy gaps. In: The ecology of natural disturbance and patch dynamics (Eds.) Pickett, S.T.A. and White, P.S. Academic Press. Orlando, Florida. Pp. 218-234.
- Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.
- DeGrandpre, L., Gagnon, D. and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. Journal of Vegetation Science 4: 803-810.
- Dyrness, C.T., Van Cleve, K., and Levinson, J.D. 1989. The effect of wildfire on soil chemistry in four forest fire types in interior Alaska. Canadian Journal of Forest Research 19: 1389-1396.

- Eberhart, K.E. and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17: 1207-1212.
- Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Fenton V., Jowsey J., and McLean J. 1984. Wildflowers of the Northern Great Plains. University of Minnesota Press. Minneapolis, Minnesota.
- Fischer, W.C. and Clayton, B.D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Intermountain Research Station, Forest Service, U.S. Department of Agriculture. Ogden, Utah.
- Flinn, M.A. and Wein, R.W. 1977. Depth of underground plant organs and theoretical survival during fire. *Canadian Journal of Botany* 55: 2550-2554.
- Foster, D.R. 1983. The history of and pattern of fire in the boreal forest of southeastern Labrador. *Canadian Journal of Botany* 61: 2459-2471.
- Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. *Journal of Ecology* 73: 517-534.
- Fryer, G.I. and Johnson, E.A. 1988. Reconstructing fire behaviour and effects in a subalpine forest. *Journal of Applied Ecology* 25: 1063-1072.
- Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703-1715.
- Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70: 704-720.
- Halpern, C.B. and Franklin, J.F. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. *Journal of Vegetation Science* 1: 475-482.
- Heinselman, M.L. 1971. The natural role of fire in northern conifer forests. In: Fire in the northern environment - a symposium (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range and Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 61-72.

- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3: 329-382.
- Hill, M.O. 1979. TWINSpan-A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Cornell University. New York, New York.
- Hill, M.O., Bunce, R.G.H. and Shaw, M.W. 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. *Journal of Ecology* 63: 597-613.
- Hoehne, L.M. 1981. The groundlayer vegetation of forest islands in an urban-suburban matrix. In: *Forest island dynamics in man-dominated landscapes* (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 41-54.
- Hornberg, G., Zackrisson, O., Segerstrom, U., Svensson, B.W., Ohlson, M. and Bradshaw, R.H.W. 1998. Boreal swamp forests - biodiversity "hotspots" in an impoverished forest landscape. *BioScience* 48: 795-802.
- Hunter, M.L. Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65: 115-120.
- Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. *Canadian Journal of Botany* 53: 2933-2941.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press. Cambridge, Great Britain.
- Jongman, R.H.G, ter Braak, C.J.F. and van Tongeren, O.F.R. 1987. *Data analysis in community and landscape ecology*. Center for Agricultural Publishing and Documentation. Pudoc Wageningen, Netherlands.
- Keane, R.E., Ryan, K.C. and Running, S.W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with ecological process model FIRE-BGC. *Tree Physiology* 16: 319-331.
- Kent, M. and Coker, P. 1992. *Vegetation description and analysis. A practical approach*. John Wiley and Sons. Toronto, Ontario.
- Kutiel, P. and Naveh, Z. 1987. The effect of fire on nutrients in a pine forest soil. *Plant and Soil* 104: 269-274.

- Lack, D. 1969. The number of bird species on islands. *Bird Study* 16: 193-209.
- Levenson, J.B. 1981. Woodlots as biogeographic islands in Southeastern Wisconsin. In: *Forest island dynamics in man-dominated landscapes* (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 13-39.
- Martin, R.E., Miller, R.L. and Cushwa, C.T. 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56: 1441-1445.
- Matlack, G.R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. *Journal of Ecology* 82: 113-123.
- McGee, G.G., Leopold, D.J. and Nyland, R.D. 1995. Understory response to spring time prescribed fire in two New York transition oak forests. *Forest Ecology and Management* 76: 149-168.
- McLean, A. 1969. Fire resistance of forest species as influenced by root systems. *Journal of Range Management* 22: 120-122.
- Michalsky, S.J. 1987. Prescribed Crown Fire Effects on a Subalpine Bighorn Sheep Range at Ram Mountain in Alberta, Canada. M.Sc. Thesis, University of Alberta. Edmonton, Alberta.
- Moore, J.M. and Wein, R.W. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* 55: 2408-2412.
- Morneau, C. and Payette, S. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. *Canadian Journal of Botany* 67: 2770-2782.
- Morris, W.G. 1958. Influence of slash burning on regeneration, other plant cover, and fire hazard in the Douglas-fir region (a progress report). Res. Pap. PNW-29. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon.
- National Soil Survey Committee of Canada. 1987. The Canadian system of soil classification. Canadian Department of Agriculture Research Publication 1946. Ottawa, Ontario.
- Payette, S., Morneau, C., Sirois, L. and Despons, M. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70: 656-673.
- Quirk, W.A. and Sykes, D.J. 1971. White spruce stringers in a fire-patterned

- landscape in interior Alaska. In: Fire in the northern environment - a symposium. (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 179-197.
- Ranney, J.W., Bruner, M.C. and Levenson, J.B. 1981. The importance of edge in structure and dynamics of forest islands. In: Forest island dynamics in man-dominated landscapes. (Eds.) Burgess, R.L. and Sharpe, D.M. Springer-Verlag. New York, New York. Pp. 67-95.
- Rapp, K., Naess, S.K. and Swartz, H.J. 1993. Commercialization of the cloudberry (*Rubus chamaemorus* L.) in Norway. In: New crops. (Eds.) Janick, J. and Simon, J.E. Wiley. New York, New York. Pp. 524-526.
- Rogeanu, M.-P. 1996. Understanding Age-Class Distributions in the Southern Canadian Rocky Mountains. M.Sc. Thesis, University of Alberta. Edmonton, Alberta.
- Romme, W.H. and Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62: 319-326.
- Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. *Canadian Journal of Botany* 39: 1007-1017.
- Rowe, J.S. and Scotter, G.W. 1973. Fire in the boreal forest. *Quaternary Research* 3: 444-464.
- Schaefer, J.A. 1993. Spatial patterns in taiga plant communities following fire. *Canadian Journal of Botany* 71: 1568-1573.
- Schimmel, J. and Granstrom, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77: 1436-1450.
- Strauss, D., Bednar, L. and Mees, R. 1989. Do one percent of fires cause ninety-nine percent of the damage? *Forest Science* 35: 319-328.
- Strickland, R.J. 1995. Fire Report Form (FP48) 1961-1982 Database Data Dictionary. Provincial Forest Fire Centre, Forest Protection Division, Land and Forest Service. <ftp://ftp.env.gov.ab.ca/jfw/Pre82DD.doc>.
- Strong W.L. and Leggat K.R. 1981. Ecoregions of Alberta. Alberta Energy and Natural Resources, ENR Technical Report Number T/4. Edmonton, Alberta.

- Swanson, F.J. and Franklin, J.F. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2: 262-274.
- Tande, G.F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. *Canadian Journal of Botany* 57: 1912-1931.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- ter Braak, C.J.F. 1988. CANOCO - a FORTRAN program for CANonical community ordination by correspondence analysis, principle components analysis, and redundancy analysis. TNO Institute of Applied Computer Science. Wageningen, Netherlands.
- ter Braak, C.J.F. 1990. Update notes: CANOCO version 3.10. Agricultural Mathematics Group. Wageningen, Netherlands.
- Van Wagner, C.E. 1967. Seasonal variation in moisture content of eastern Canadian tree foliage and the possible effect on crown fires. Minister of Forestry and Rural Development, Forestry Branch, Departmental Publication No. 1204. Ottawa, Ontario.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *The Botanical Review* 45: 229-299.
- Wein, R.W. and MacLean, D.A. (Eds.). 1983. The role of fire in northern circumpolar ecosystems. John Wiley and Sons. New York, New York.
- Wright, H.A. and Bailey, A.W. 1982. Fire Ecology United States and Southern Canada. John Wiley and Sons. New York, New York.
- Wright, H.E. Jr. and Heinzelman, M.L. 1973. The ecological role of fire in natural conifer forests of western and northern America. *Quaternary Research* 3: 317-328.
- Zasada, J.C. 1971. Natural regeneration of interior Alaska forests - seed, seedbed, and vegetative reproduction characteristics. In: Fire in the northern environment - a symposium. (Eds.) Slaughter, C.W., Barney, R.J. and Hansen, G.M. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. Portland, Oregon. Pp. 231-246.

Table 2.1 Number and corresponding sizes of fire skips in the study site.

Fire Skip Number	Fire Skip Size (ha)	Fire Skip Number	Fire Skip Size (ha)	Fire Skip Number	Fire Skip Size (ha)
1	0.0006	16	0.0547	32	0.5428
2	0.0083	17	0.0596	33	0.5942
3	0.0103	18	0.0679	34	0.6082
4	0.0122	19	0.0733	35	0.9128
5	0.0131	20	0.0886	36	0.9736
6	0.0152	21	0.1012	37	1.0032
7	0.0169	22	0.1262	38	1.0238
8	0.0185	23	0.1317	39	1.2745
9	0.0254	24	0.1675	40	1.5651
10	0.0276	25	0.2408	41	1.6767
11	0.0329	26	0.2602	42	1.7532
12	0.0356	27	0.2839	43	1.9704
13	0.0389	28	0.3796	44	7.3113
14	0.0461	29	0.3938	45	7.7665
15	0.0472	30	0.4232	46	10.9236
		31	0.4990	Burn	1291.45

Table 2.2 Description of treatments and corresponding number of samples and sub-samples.

Treatments	Description	Number of samples (transects)	Number of sub- samples (quadrats)
1	Core areas of fire skips	*+27	302
2	Inside edge areas within the fire skips	*8	112
3	Outside edge around each fire skip	*11	127
4	Unburned lodgepole pine forest	8	100
5	Unburned Englemann spruce/white spruce forest	5	50
6	Burned area of the fire	13	123
7	Burned riparian areas of the fire	4	30
Total+		76	844

* These samples were averaged to one sample per fire skip.

+ Does not include riparian areas associated with skips 1, 2 and 4.

Table 2.3 Description of samples (transects) used in DCA analysis.

Transect/ Sample	Transect/ Sample	Identification
Number	Identifier	
1	LS1 CTS	Large Skip 1 Core Transects*
2	LS2 CTS	Large Skip 2 Core Transects*
3	MS1 CTS	Medium Skip 1 Core Transects*
4	MS2 CTS	Medium Skip 2 Core Transects*
5	SS1 CTS	Small Skip 1 Core Transects*
6	SS2 CTS	Small Skip 2 Core Transects*
7	SS3 CTS	Small Skip 3 Core Transects*
8	LP1 TT1	Lodgepole Pine Transect 1
9	LP1 TT2	Lodgepole Pine Transect 2
10	LP1 TT3	Lodgepole Pine Transect 3
11	LP2 TT4	Lodgepole Pine Transect 4
12	LP3 TT5	Lodgepole Pine Transect 5
13	LP4 TT6	Lodgepole Pine Transect 6
14	LP4 TT7	Lodgepole Pine Transect 7
15	LP5 TT8	Lodgepole Pine Transect 8
16	ES1 TT1	Englemann Spruce Transect 1
17	ES1 TT2	Englemann Spruce Transect 2
18	ES2 TT3	Englemann Spruce Transect 3
19	ES2 TT4	Englemann Spruce Transect 4
20	ES3 TT5	Englemann Spruce Transect 5
21	BU1 T01	Burned Transect 1
22	BU1 T02	Burned Transect 2
23	BU2 T03	Burned Transect 3
24	BU2 T04	Burned Transect 4
25	BU3 T05	Burned Transect 5
26	BU3 T06	Burned Transect 6
27	BU3 T07	Burned Transect 7
28	BU4 T08	Burned Transect 8
29	BU5 T09	Burned Transect 9
30	BU6 T10	Burned Transect 10
31	BU7 T11	Burned Transect 11
32	BU7 T12	Burned Transect 12
33	BU7 T13	Burned Transect 13
34	LS1 ITS	Large Skip 1 Inside Transects*+
35	LS1 OTS	Large Skip 1 Outside Transects*+
36	LS2 ITS	Large Skip 2 Inside Transects*+
37	LS2 OTS	Large Skip 2 Outside Transects*+
38	MS1 ITS	Medium Skip 1 Inside Transects*+
39	MS1 OTS	Medium Skip 1 Outside Transects*+
40	MS2 ITS	Medium Skip 2 Inside Transects*+
41	MS2 OTS	Medium Skip 2 Outside Transects*+
42	SS1 OTS	Small Skip 1 Outside Transects*+
43	SS2 OTS	Small Skip 2 Outside Transects*+
44	SS3 OTS	Small Skip 3 Outside Transects*+

* Denotes sample is an average of the various transects of the skips.

+ Denotes sample does not have all external factor data to be used in a DCA analysis.

Table 2.4 Average cover for measured species.

Species	Average Cover	Standard Deviation
<i>Achillea millefolium</i>	0.022	0.279
<i>Arnica angustifolia</i>	0.028	0.714
<i>Arnica cordifolia</i>	1.102	3.802
<i>Arnica latifolia</i>	0.317	2.379
<i>Aster modestus</i>	0.018	0.530
<i>Aster species</i>	0.020	0.564
<i>Aster subspicatus</i>	0.007	0.148
<i>Caltha leptosepala</i>	0.013	0.364
<i>Campanula lasiocarpa</i>	0.005	0.165
<i>Cassiope tetragona</i>	0.003	0.099
<i>Chrysosplenium tetrandrum</i>	0.012	0.364
<i>Cornus canadensis</i>	4.434	6.523
<i>Epilobium angustifolium</i>	0.559	4.088
<i>Epilobium ciliatum</i>	0.485	2.219
<i>Equisetum arvense</i>	0.031	0.479
<i>Equisetum palustre</i>	0.017	0.436
<i>Equisetum pratense</i>	0.923	4.454
<i>Equisetum scirpoides</i>	0.376	1.907
<i>Equisetum sylvaticum</i>	0.648	3.591
<i>Erigeron humilis</i>	0.132	1.176
<i>Fragaria virginiana</i>	0.065	1.044
<i>Gentiana glauca</i>	0.004	0.132
<i>Gentianella propinqua</i>	0.007	0.148
<i>Goodyera repens</i>	0.002	0.066
<i>Habenaria obtusata</i>	0.008	0.145
<i>Halenia deflexa</i>	0.003	0.068
<i>Hieracium albiflorum</i>	0.022	0.327
<i>Hieracium gracile</i>	0.094	0.917
<i>Hieracium species</i>	0.009	0.265
<i>Linnaea borealis</i>	1.134	3.595
<i>Listera cordata</i>	0.300	3.164
<i>Lupinus nootkatensis</i>	0.096	1.561
<i>Maianthemum canadense</i>	0.089	1.187
<i>Mertensia paniculata</i>	0.051	0.766
<i>Mitella nuda</i>	0.327	1.315
<i>Mitella pentandra</i>	0.164	1.267
<i>Moneses uniflora</i>	0.117	0.839
<i>Orthilia secunda</i>	0.119	0.786
<i>Parnassia fimbriata</i>	0.133	1.194
<i>Pedicularis labridorica</i>	0.016	0.376
<i>Pedicularis racemosa</i>	0.042	0.466
<i>Petasites frigidus</i>	0.355	2.305
<i>Petasites palmatus</i>	0.360	1.613
<i>Polygonum viviparum</i>	0.134	0.653
<i>Pyrola virens</i>	0.068	0.752

Table 2.4 Average cover for measured species (continued).

Species	Average Cover	Standard Deviation
<i>Ranunculus nivalis</i>	0.002	0.066
<i>Ranunculus uncinatus</i>	0.482	2.098
<i>Rubus acaulis</i>	0.044	0.672
<i>Rubus chamaemorus</i>	0.319	2.924
<i>Rubus pedatus</i>	2.459	4.212
<i>Rubus pubescens</i>	0.013	0.260
<i>Saxifraga lyallii</i>	0.080	1.143
<i>Senecio triangularis</i>	0.329	2.128
<i>Smilacina racemosa</i>	0.010	0.179
<i>Stellaria calycantha</i>	0.005	0.099
<i>Streptopus amplexifolius x oreopolus</i>	0.037	0.776
<i>Taraxacum officinale</i>	0.004	0.094
<i>Tiarella unifoliata</i>	0.055	0.697
<i>Valeriana sitchensis</i>	0.077	0.882
<i>Veronica americana</i>	0.001	0.033
<i>Calamagrostis canadensis</i>	0.222	1.507
<i>Calamagrostis inexpansa</i>	0.357	2.878
<i>Carex leptalea</i>	0.055	0.569
<i>Carex phaeocephala</i>	0.013	0.296
<i>Carex species</i>	0.018	0.214
<i>Cinna latifolia</i>	0.007	0.148
<i>Deschampsia atropurpurea</i>	1.203	4.532
<i>Elymus innovatus</i>	0.021	0.316
Grass species	0.007	0.199
<i>Hierochloa odorata</i>	0.005	0.119
<i>Poa species</i>	0.112	1.488
<i>Trisetum spicatum</i>	0.002	0.066
<i>Abies lasiocarpa</i>	9.217	14.374
<i>Alnus tenuifolia</i>	0.009	0.265
<i>Arctostaphylos uva-ursi</i>	0.007	0.199
<i>Betula glandulosa</i>	3.044	11.265
<i>Empetrum nigrum</i>	4.965	11.038
<i>Kalmia polifolia</i>	0.008	0.166
<i>Ledum groenlandicum</i>	2.526	8.226
<i>Lonicera dioica</i>	0.579	3.817
<i>Lonicera involucrata</i>	2.427	7.847
<i>Phyllodoce empetriformis</i>	0.028	0.541
<i>Picea englemanni</i>	0.354	3.851
<i>Pinus contorta</i>	0.120	1.502
<i>Populus tremuloides</i>	0.029	0.374
<i>Rhododendron albiflorum</i>	6.574	16.235
<i>Ribes glandulosum</i>	0.153	1.499
<i>Ribes hudsonianum</i>	1.688	8.630
<i>Ribes lacustre</i>	0.269	1.854
<i>Ribes oxycanthoides</i>	0.049	0.652

Table 2.4 Average cover for measured species (continued).

Species	Average Cover	Standard Deviation
<i>Rosa acicularis</i>	0.054	0.726
<i>Rubus idaeus</i>	0.079	0.848
<i>Salix bebbiana</i>	0.381	3.074
<i>Salix commutata</i>	0.133	1.822
<i>Salix drummondiana</i>	0.760	4.481
<i>Salix glauca</i>	0.513	6.117
<i>Salix lucida</i> ssp. <i>lassiandra</i>	1.104	7.700
<i>Salix maccalliana</i>	0.077	1.071
<i>Salix planifolia</i>	0.778	6.490
<i>Salix pseudomonticola</i>	0.024	0.695
<i>Salix sitchensis</i>	0.115	1.463
<i>Salix</i> species	0.441	3.526
<i>Sorbus scopulina</i>	0.055	0.789
<i>Vaccinium membranaceum</i>	7.910	13.712
<i>Vaccinium myrtilloides</i>	1.541	6.442
<i>Vaccinium vitis-idaea</i>	0.742	2.227
<i>Aulacomnium palustre</i>	3.208	9.777
<i>Barbilophozia lycopodioides</i>	3.098	7.779
<i>Brachythecium</i> species	3.825	13.356
<i>Dicranum polysetum</i>	1.516	6.356
<i>Dicranum scoparium</i>	3.041	8.850
<i>Dicranum undulatum</i>	0.096	1.028
<i>Drepanocladus aduncus</i>	0.113	1.852
<i>Drepanocladus uncinatus</i>	0.733	4.946
<i>Hylocomium splendens</i>	16.691	26.281
<i>Lophozia ventricosa</i>	0.001	0.017
<i>Lycopodium annotinum</i>	0.512	2.375
<i>Lycopodium complanatum</i>	0.013	0.241
<i>Pellia neesiana</i>	0.032	0.466
<i>Plagiomnium medium</i>	1.176	5.318
<i>Pleurozium schreberi</i>	18.469	26.963
<i>Pogonatum alpinum</i>	0.002	0.066
<i>Pohlia nutans</i>	0.183	1.629
<i>Polytrichum commune</i>	0.367	3.656
<i>Polytrichum juniperinum</i>	1.530	7.654
<i>Polytrichum piliferum</i>	0.085	1.383
<i>Polytrichum strictum</i>	3.192	12.984
<i>Ptilium crista-castrensis</i>	5.191	14.339
<i>Rhizomnium glabrescens</i>	1.314	6.162
<i>Sphagnum angustifolium</i>	2.464	10.837
<i>Sphagnum fuscum</i>	0.430	5.334
<i>Sphagnum girgensohnii</i>	0.520	4.090
<i>Sphagnum magellanicum</i>	0.107	1.589
<i>Tomenthypnum nitens</i>	0.177	2.289
<i>Tortula ruralis</i>	0.001	0.033

Table 2.4 Average cover for measured species (continued).

Species	Average Cover	Standard Deviation
<i>Tomenthypnum nitens</i>	0.177	2.289
<i>Tortula ruralis</i>	0.001	0.033
<i>Cetraria cucullata</i>	0.001	0.023
<i>Cladina mitis</i>	0.099	1.247
<i>Cladina rangiferina</i>	0.124	0.916
<i>Cladonia</i> species	0.705	2.248
<i>Icmadophila ericetorum</i>	0.004	0.132
<i>Lobaria linita</i>	0.735	3.980
<i>Lobaria pulmonaria</i>	2.947	11.461
<i>Peltigera aphthosa</i>	0.929	3.577
<i>Peltigera canina</i>	0.364	2.688
<i>Peltigera didactyla</i>	0.053	1.282
<i>Peltigera leucophlebia</i>	0.018	0.362
<i>Peltigera malacea</i>	0.003	0.099
<i>Peltigera neopolydactyla</i>	0.472	2.235
<i>Stereocaulon alpinum</i>	0.065	0.861
Average	1.055	3.246

Table 2.5 Summary of understory plant species cover and other environmental factors in the 6 community types from TWINSpan.

Species	Percent Cover/Plant Community Types					
	ES	LP	FSC	LSE	MSE	BU
Forbs						
<i>Achillea millefolium</i>	0.06	0.00	0.00	0.00	0.00	0.01
<i>Arnica angustifolia</i>	0.03	0.00	0.00	0.18	0.00	0.00
<i>Arnica cordifolia</i>	2.13	0.70	0.83	0.58	0.86	0.05
<i>Arnica latifolia</i>	0.26	0.75	0.00	0.19	0.00	0.00
<i>Aster modestus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Aster species</i>	0.00	0.00	0.00	0.15	0.00	0.01
<i>Aster subspicatus</i>	0.00	0.00	0.00	0.00	0.00	0.05
<i>Caltha leptosepala</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Campanula lasiocarpa</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cassiope tetragona</i>	0.00	0.00	0.00	0.03	0.00	0.00
<i>Chrysosplenium tetrandrum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Cornus canadensis</i>	4.13	4.76	3.50	5.85	8.89	0.00
<i>Epilobium angustifolium</i>	0.08	0.30	0.00	0.32	1.73	0.00
<i>Epilobium ciliatum</i>	0.00	0.00	0.00	0.05	0.05	2.89
<i>Equisetum arvense</i>	0.00	0.00	0.06	0.14	0.00	0.00
<i>Equisetum palustre</i>	0.09	0.00	0.00	0.00	0.00	0.00
<i>Equisetum pratense</i>	2.67	0.00	0.02	0.21	0.00	0.00
<i>Equisetum scirpoides</i>	0.61	0.00	0.42	0.14	0.00	0.68
<i>Equisetum sylvaticum</i>	2.26	0.28	0.49	0.34	0.36	0.02
<i>Erigeron humilis</i>	0.00	0.02	0.00	0.00	0.00	0.96
<i>Fragaria virginiana</i>	0.31	0.00	0.00	0.01	0.00	0.00
<i>Gentiana glauca</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gentianella propinqua</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Goodyera repens</i>	0.01	0.00	0.00	0.00	0.00	0.00
<i>Habenaria obtusata</i>	0.02	0.00	0.00	0.00	0.00	0.03
<i>Halenia deflexa</i>	0.02	0.00	0.00	0.00	0.00	0.00
<i>Hieracium albiflorum</i>	0.13	0.00	0.01	0.00	0.00	0.00
<i>Hieracium gracile</i>	0.07	0.00	0.00	0.00	0.00	0.62
<i>Hieracium species</i>	0.00	0.00	0.04	0.00	0.00	0.00
<i>Linnaea borealis</i>	2.88	1.11	0.99	0.97	0.41	0.00
<i>Listera cordata</i>	0.24	0.02	0.07	0.00	0.00	1.79
<i>Lupinus nootkatensis</i>	0.00	0.41	0.00	0.12	0.00	0.00
<i>Maianthemum canadense</i>	0.27	0.12	0.02	0.03	0.00	0.13
<i>Mertensia paniculata</i>	0.05	0.00	0.01	0.07	0.00	0.00
<i>Mitella nuda</i>	0.99	0.05	0.30	0.18	0.08	0.07
<i>Mitella pentandra</i>	0.28	0.07	0.00	0.05	0.13	0.24
<i>Moneses uniflora</i>	0.17	0.02	0.02	0.02	0.00	0.08
<i>Orthilia secunda</i>	0.24	0.09	0.15	0.00	0.14	0.00
<i>Parnassia fimbriata</i>	0.08	0.00	0.00	0.13	0.00	0.00
<i>Pedicularis labridorica</i>	0.01	0.00	0.00	0.02	0.00	0.00
<i>Pedicularis racemosa</i>	0.08	0.00	0.00	0.06	0.00	0.01
<i>Petasites frigidus</i>	0.31	0.05	0.03	0.08	0.19	0.00
<i>Petasites palmatus</i>	0.93	0.21	0.24	0.21	0.00	0.09

Table 2.5 Summary of understory plant species cover and other environmental factors in the 6 community types from TWINSpan (continued).

Species	Percent Cover/Plant Community Types					
	ES	LP	FSC	LSE	MSE	BU
<i>Polygonum viviparum</i>	0.00	0.00	0.03	0.00	0.00	0.00
<i>Pyrola virens</i>	0.02	0.00	0.13	0.00	0.00	0.00
<i>Ranunculus nivalis</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Ranunculus uncinatus</i>	0.48	0.00	0.12	0.14	0.03	0.07
<i>Rubus acaulis</i>	0.00	0.11	0.03	0.00	0.00	0.07
<i>Rubus chamaemorus</i>	1.76	0.00	0.01	0.00	0.00	0.02
<i>Rubus pedatus</i>	1.86	2.89	2.42	3.09	6.89	0.00
<i>Rubus pubescens</i>	0.00	0.00	0.00	0.06	0.00	0.04
<i>Saxifraga lyallii</i>	0.01	0.00	0.00	0.00	0.00	0.00
<i>Senecio triangularis</i>	0.23	0.00	0.00	0.00	0.00	2.13
<i>Smilacina racemosa</i>	0.00	0.00	0.00	0.00	0.00	0.08
<i>Stellaria calycantha</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Streptopus amplexifolius</i> **	0.00	0.00	0.00	0.00	0.00	0.00
<i>Taraxacum officinale</i>	0.00	0.00	0.00	0.00	0.00	0.02
<i>Tiarella unifoliata</i>	0.04	0.07	0.10	0.10	0.00	0.00
<i>Valeriana sitchensis</i>	0.26	0.00	0.00	0.00	0.25	0.00
<i>Veronica americana</i>	0.00	0.00	0.00	0.00	0.00	0.00
Grasses						
<i>Calamagrostis canadensis</i>	0.14	0.06	0.00	0.11	0.28	0.00
<i>Calamagrostis inexpansa</i>	0.00	0.00	0.00	0.00	0.00	2.62
<i>Carex leptalea</i>	0.18	0.00	0.00	0.00	0.00	0.00
<i>Carex phaeocephala</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Carex species</i>	0.05	0.00	0.02	0.00	0.00	0.00
<i>Cinna latifolia</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Deschampsia atropurpurea</i>	0.03	0.00	0.00	0.03	0.03	8.29
<i>Elymus innovatus</i>	0.01	0.08	0.00	0.00	0.00	0.03
<i>Grass species</i>	0.00	0.00	0.03	0.00	0.00	0.00
<i>Hierochloe odorata</i>	0.00	0.00	0.00	0.00	0.00	0.02
<i>Poa species</i>	0.15	0.00	0.00	0.00	0.00	0.41
<i>Trisetum spicatum</i>	0.00	0.00	0.00	0.00	0.00	0.02
Shrubs						
<i>Abies lasiocarpa</i>	10.72	9.15	14.56	9.23	6.56	0.00
<i>Alnus tenuifolia</i>	0.00	0.00	0.00	0.07	0.00	0.00
<i>Arctostaphylos uva-ursi</i>	0.00	0.00	0.00	0.00	0.00	0.05
<i>Betula glandulosa</i>	0.08	0.56	0.00	0.00	0.00	21.50
<i>Empetrum nigrum</i>	3.83	11.33	3.54	6.55	4.70	1.10
<i>Kalmia polifolia</i>	0.00	0.00	0.00	0.00	0.00	0.06
<i>Ledum groenlandicum</i>	3.33	6.43	2.62	1.49	0.00	0.08
<i>Lonicera dioica</i>	0.20	0.00	0.00	0.00	0.00	4.05
<i>Lonicera involucrata</i>	0.20	0.00	0.00	0.00	0.78	16.70
<i>Phyllodoce empetriformis</i>	0.10	0.00	0.00	0.10	0.00	0.00
<i>Picea englemannii</i>	0.10	0.14	0.94	0.29	0.11	0.27
<i>Pinus contorta</i>	0.00	0.03	0.00	0.66	0.00	0.00

Table 2.5 Summary of understory plant species cover and other environmental factors in the 6 community types from TWINSpan (continued).

Species	Percent Cover/Plant Community Types					
	ES	LP	FSC	LSE	MSE	BU
<i>Populus tremuloides</i>	0.00	0.01	0.00	0.00	0.00	0.20
<i>Rhododendron albiflorum</i>	0.79	7.52	9.50	9.64	19.77	2.58
<i>Ribes glandulosum</i>	0.14	0.00	0.00	0.32	0.77	0.04
<i>Ribes hudsonianum</i>	0.31	0.00	0.02	0.20	0.39	10.22
<i>Ribes lacustre</i>	0.37	0.00	0.02	0.31	0.00	0.30
<i>Ribes oxycanthoides</i>	0.00	0.00	0.02	0.20	0.00	0.14
<i>Rosa acicularis</i>	0.27	0.05	0.00	0.00	0.00	0.00
<i>Rubus idaeus</i>	0.02	0.00	0.00	0.02	0.50	0.00
<i>Salix bebbiana</i>	0.26	0.00	0.00	0.25	0.00	0.00
<i>Salix commutata</i>	0.25	0.00	0.05	0.10	0.00	0.03
<i>Salix drummondiana</i>	0.00	0.00	0.00	0.54	0.00	3.19
<i>Salix glauca</i>	0.05	0.00	0.23	0.00	0.00	3.38
<i>Salix lucida</i> asp. <i>lassiandra</i>	1.74	0.07	0.35	0.78	0.00	0.00
<i>Salix maccalliana</i>	0.00	0.40	0.00	0.00	0.00	0.00
<i>Salix planifolia</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Salix pseudomonticola</i>	0.00	0.00	0.00	0.00	0.00	1.30
<i>Salix sitchensis</i>	0.00	0.00	0.00	0.00	0.00	0.52
<i>Salix species</i>	0.56	0.00	1.29	0.59	0.00	0.00
<i>Sorbus scopulina</i>	0.00	0.19	0.00	0.12	0.00	0.00
<i>Vaccinium membranaceum</i>	3.29	12.63	10.58	9.41	17.42	0.07
<i>Vaccinium myrtilloides</i>	0.29	4.51	1.52	0.64	0.00	1.59
<i>Vaccinium vitis-idaea</i>	1.00	1.97	0.36	0.73	0.00	0.24
Mosses						
<i>Aulacomnium palustre</i>	8.27	0.49	1.37	1.78	1.91	1.62
<i>Barbilophozia lycopodioides</i>	3.83	1.93	3.95	4.97	7.25	0.08
<i>Brachythecium species</i>	0.00	0.00	0.01	0.18	0.80	25.81
<i>Dicranum polysetum</i>	0.81	1.86	0.45	4.01	4.88	0.54
<i>Dicranum scoparium</i>	1.40	5.48	3.02	7.26	2.59	0.07
<i>Dicranum undulatum</i>	0.00	0.20	0.00	0.00	0.16	0.35
<i>Drepanocladus aduncus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Drepanocladus uncinatus</i>	0.37	0.00	0.04	0.47	0.00	0.00
<i>Hylacomium splendens</i>	35.23	10.06	26.70	10.30	17.95	0.00
<i>Lophozia ventricosa</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lycopodium annotinum</i>	0.78	0.37	0.98	0.15	1.00	0.00
<i>Lycopodium complanatum</i>	0.00	0.00	0.00	0.00	0.00	0.09
<i>Pellia neesiana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Plagiomnium medium</i>	1.52	0.00	0.64	0.10	0.13	0.11
<i>Pleurozium schreberi</i>	10.83	35.92	28.67	14.36	19.18	0.86
<i>Pogonatum alpinum</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pohlia nutans</i>	0.06	0.11	0.00	0.82	0.70	0.00
<i>Polytrichum commune</i>	0.22	0.22	0.24	0.08	1.82	0.00
<i>Polytrichum juniperinum</i>	0.78	1.51	0.61	3.13	2.77	1.95
<i>Polytrichum piliferum</i>	0.00	0.00	0.00	0.28	0.00	0.35
<i>Polytrichum strictum</i>	0.10	0.02	0.00	0.00	0.00	23.18

Table 2.5 Summary of understory plant species cover and other environmental factors in the 6 community types from TWINSpan (continued).

Species	Percent Cover/Plant Community Types					
	ES	LP	FSC	LSE	MSE	BU
<i>Ptilium crista-castrensis</i>	6.63	5.53	9.64	3.73	5.45	0.11
<i>Rhizomnium glabrescens</i>	1.15	0.00	0.00	0.42	0.16	0.00
<i>Sphagnum angustifolium</i>	7.00	2.18	2.08	0.55	0.00	0.00
<i>Sphagnum fuscum</i>	0.79	0.29	1.09	0.00	0.00	0.11
<i>Sphagnum girgensohnii</i>	1.34	0.73	0.03	0.12	0.00	0.02
<i>Sphagnum magellanicum</i>	0.00	0.00	0.00	0.00	0.00	0.79
<i>Tomenthypnum nitens</i>	0.94	0.00	0.00	0.00	0.00	0.00
<i>Tortula ruralis</i>	0.01	0.00	0.00	0.00	0.00	0.00
Lichens						
<i>Cetraria cucullata</i>	0.00	0.00	0.00	0.00	0.01	0.00
<i>Cladonia mitis</i>	0.01	0.18	0.05	0.38	0.05	0.00
<i>Cladonia rangerifera</i>	0.00	0.29	0.11	0.24	0.05	0.08
<i>Cladonia species</i>	0.25	0.78	0.94	1.18	0.96	0.63
<i>Imadophila ericetorum</i>	0.00	0.02	0.00	0.00	0.00	0.00
<i>Lobaria linita</i>	0.04	0.63	1.83	1.25	0.30	0.00
<i>Lobaria pulmonaria</i>	0.00	0.00	0.04	0.00	0.00	21.82
<i>Peltigera aphthosa</i>	1.34	0.79	1.28	1.21	1.22	0.00
<i>Peltigera canina</i>	0.27	1.31	0.18	0.20	0.00	0.00
<i>Peltigera didactyla</i>	0.00	0.00	0.00	0.06	0.00	0.02
<i>Peltigera leucophlebia</i>	0.00	0.00	0.06	0.00	0.00	0.03
<i>Peltigera malacea</i>	0.02	0.00	0.00	0.00	0.00	0.00
<i>Peltigera neopolydactyla</i>	0.55	0.75	0.16	0.71	0.94	0.00
<i>Stereocaulon alpinum</i>	0.00	0.11	0.00	0.08	0.02	0.18
Others Factors						
Bare Ground	0.44	0.58	0.23	6.34	3.02	8.43
Litter	10.06	18.56	6.57	13.27	18.19	0.53
Fallen Wood	8.11	5.82	7.11	10.73	10.51	7.75
Total Cover	137.08	138.93	139.85	113.93	141.59	167.96
Total Species Richness	95	64	70	80	47	77
Species Diversity*	3.15	2.84	2.73	3.20	2.81	2.77
Species Evenness*	0.69	0.68	0.64	0.73	0.73	0.64

TWINSpan community types: ES = Englemann Spruce,

LP = lodgepole pine, FSC = fire skip cores, LSE = large skip edges,

MSE = medium skip edges, BU = burned.

* Denotes calculated values not percent cover values.

** Denotes *Streptopus amplexifolius x oreopolus*.

Table 2.6 Results of the forward selection of ordination centroids ("treatments") from a CCA with their approximate significance, and canonical coefficients and intraset correlations for the first two axes.

Treatment Centroids	Spp. - Env. Variance Expl.	Significance of M.C. Test	Axis 1		Axis 2	
			CCA Coef.	Intraset	CCA Coef.	Intraset
Large Core	4%	P=0.18	-0.712	-4.9	0.150	10.5
Medium Core	n/a*	n/a*	-0.722	-4.8	0.100	-7.2
Small Core	14%	p<0.01	-0.723	-5.1	-0.091	-6.6
Pine Forest	14%	p<0.01	-0.772	-5.4	-0.641	-47.6
Spruce Forest	11%	p<0.01	-0.642	-4.2	0.646	44.8
Burned Area	57%	p<0.01	0.000	17.3	0.000	-0.1

* Denotes last variable is selected by default.

Table 2.7 Summary of understory plant species cover and other external factors for the 7 stratified treatment types.

	Percent Cover / Plant Community Types						
	LS	MS	SS	LP	ES	BU	BUR
Bare Ground	0.3	0.1	0.0	0.2	0.4	8.4	1.6
Litter	5.8	5.3	12.8	23.8	13.9	0.5	23.1
Fallen Wood	7.8	6.7	5.6	5.9	4.1	7.7	3.3
Total Cover	133.8	147.7	136.9	131.0	135.1	168.0	165.3
Total Species R	110	41	42	53	74	77	68
Species Diversi	3.02	2.61	2.77	2.64	3.11	2.77	3.54
Species Evenes	0.64	0.70	0.74	0.66	0.72	0.64	0.84
Average Age	232	227	126	106	226	143	N/A*
Organic Matte	10.76	9.75	14.49	3.32	16.30	2.16	N/A*
Average Slope*	20.94	9.87	2.50	4.03	0.72	5.79	N/A*
Tree Volume/h	239.25	133.72	138.53	243.02	421.58	N/A	N/A*
Tree Density/h	4907.69	6147.94	6760.84	5291.27	3498.41	7076.71	N/A*

Treatments (for skips, excludes edges and riparian areas): LS = large skips

MS = medium skips, SS = small skips, LP = lodgepole pine, ES = Englemann spruce

BU = burned, BUR = burned riparian.

* Denotes N/A = not available.

** Denotes calculated values.

Table 2.8 Euclidian Disimilarity Indices comparisons.

Comparison	Similarity Value
Lodgepole pine to Englemann spruce	50.0
Lodgepole pine to Large Skips	37.8
Lodgepole pine to Medium Skips	30.5
Lodgepole pine to Small Skips	32.0
Englemann spruce to Large Skips	19.9
Englemann spruce to Medium Skips	37.5
Englemann spruce to Small Skips	43.8
Large Skips to Medium Skips	20.3
Large Skips to Small Skips	33.8
Medium Skips to Small Skips	33.4
Riparian Burned to Core Riparian	45.0
Burned to Core Non-Burned	62.7

Table 2.9 Euclidian Dissimilarity Indices comparisons between the burned area, large, medium and small skip cores and edges.

	LSC	LSI	LSO	BU
LSC		^^	^^	^^
LSI	6.2		^^	^^
LSO	7.6	3.7		^^
BU	64.4	63.3	61.6	
	MSC	MSI	MSO	BU
MSC		^^	^^	^^
MSI	25.8		^^	^^
MSO	25.4	7.1		^^
BU	70.7	67.1	64.4	
	SSC	SSO	BU	
SSC		^^	^^	
SSO	24.5		^^	
BU	65.6	61.4		

LSC = large skip core transects,

LSI = large skip inside transects,

LSO = large skip outside transects,

MSC = medium skip core transects,

MSI = medium skip Inside transects,

MSO = medium skip outside transects,

SSC = small skip core transects,

SSO = small skip inside transects,

BU = burned transects.

Table 2.10 Latin and common names of understory plant species.

Latin Names	Common Names
Forbs	
<i>Achillea millefolium</i>	common yarrow
<i>Arnica angustifolia</i>	alpine arnica
<i>Arnica cordifolia</i>	heart-leaved arnica
<i>Arnica latifolia</i>	mountain arnica
<i>Aster</i> species	aster species
<i>Aster modestus</i>	great northern aster
<i>Aster subspicatus</i>	Douglas' aster
<i>Caltha leptosepala</i>	alpine white marsh-marigold
<i>Campanula lasiocarpa</i>	mountain harebell
<i>Cassiope tetragona</i>	four-angled mountain-heather
<i>Chrysosplenium tetrandrum</i>	northern water-carpet
<i>Cornus canadensis</i>	bunchberry
<i>Epilobium angustifolium</i>	fireweed
<i>Epilobium ciliatum</i>	purple-leaved willowherb
<i>Equisetum arvense</i>	common horsetail
<i>Equisetum palustre</i>	marsh horsetail
<i>Equisetum pratense</i>	meadow horsetail
<i>Equisetum scirpoides</i>	dwarf scouring rush
<i>Equisetum sylvaticum</i>	wood horsetail
<i>Erigeron humilis</i>	arctic daisy
<i>Fragaria virginiana</i>	wild strawberry
<i>Gentiana glauca</i>	inky gentain
<i>Gentianella propinqua</i>	four-parted gentain
<i>Goodyera repens</i>	dwarf rattlesnake-plantain
<i>Habenaria obtusata</i>	one-leaved rein-orchid
<i>Halenia deflexa</i>	spurred gentain
<i>Hieracium albiflorum</i>	white-flowered hawkweed
<i>Hieracium gracile</i>	slender hawkweed
<i>Hieracium</i> species	hawkweed species
<i>Linnaea borealis</i>	twinflower
<i>Listera cordata</i>	heart-leaved twayblade
<i>Lupinus nootkatensis</i>	Nootka lupine
<i>Maianthemum canadense</i>	wild lily-of-the-valley
<i>Mertensia paniculata</i>	tall bluebell
<i>Mitella nuda</i>	common mitrewort
<i>Mitella pentandra</i>	five-stamened mitrewort
<i>Moneses uniflora</i> (<i>Pyrola uniflora</i>)	single delight
<i>Orthilia secunda</i>	one-sided wintergreen
<i>Parnassia fimbriata</i>	fringed grass-of-parnassus
<i>Pedicularis labridorica</i>	Labrador lousewort
<i>Pedicularis racemosa</i>	sickle-top lousewort
<i>Petasites frigidus</i>	sweet coltsfoot
<i>Petasites palmatus</i>	palmate coltsfoot
<i>Polygonum viviparum</i>	alpine bistort

Table 2.10 Latin and common names of understory plant species (continued).

Latin Names	Common Names
<i>Pyrola virens</i>	green wintergreen
<i>Ranunculus nivalis</i>	snow buttercup
<i>Ranunculus uncinatus</i>	little buttercup
<i>Rubus acaulis</i>	dwarf nagoonberry
<i>Rubus chamaemorus</i>	cloudberry
<i>Rubus pedatus</i>	five-leaved bramble
<i>Rubus pubescens</i>	trailing raspberry
<i>Saxifraga lyallii</i>	red-stemmed saxifrage
<i>Senecio triangularis</i>	arrow-leaved groundsel
<i>Smilacina racemosa</i>	false solomon's-seal
<i>Stellaria calycantha</i>	northern starwort
<i>Streptopus amplexifolius x oreopolus</i>	clasping twisted-stalk
<i>Taraxacum officinale</i>	common dandelion
<i>Tiarella unifoliata</i>	three-leaved foamflower
<i>Valeriana sitchensis</i>	Sitka valerian
<i>Veronica americana</i>	american brooklime
Grasses	
<i>Calamagrostis canadensis</i>	marsh reed grass
<i>Calamagrostis inexpansa</i>	northern reed grass
<i>Carex leptalea</i>	bristle-stalked sedge
<i>Carex phaeocephala</i>	dunhead sedge
<i>Carex</i> species	sedge species
<i>Cinna latifolia</i>	nodding wood-reed
<i>Deschampsia atropurpurea</i>	mountain hairgrass
<i>Elymus innovatus</i>	hairy wildrye
<i>Hierochloa odorata</i>	common sweetgrass
<i>Poa</i> species	bluegrasses
<i>Trisetum spicatum</i>	spike trisetum
Shrubs	
<i>Abies lasiocarpa</i>	subalpine fir
<i>Alnus tenuifolia</i>	mountain alder
<i>Arctostaphylos uva-ursi</i>	bearberry
<i>Betula glandulosa</i>	bog birch
<i>Empetrum nigrum</i>	crowberry
<i>Kalmia polifolia</i>	bog-laurel
<i>Ledum groenlandicum</i>	Labrador tea
<i>Lonicera dioica</i>	red honeysuckle
<i>Lonicera involucrata</i>	black twinberry
<i>Phyllodoce empetriformis</i>	pink mountain-heather
<i>Picea englemannii</i>	Englemann spruce
<i>Pinus contorta</i>	lodgepole pine
<i>Populus tremuloides</i>	trembling aspen
<i>Rhododendron albiflorum</i>	white-flowered rhododendron

Table 2.10 Latin and common names of understory plant species (continued).

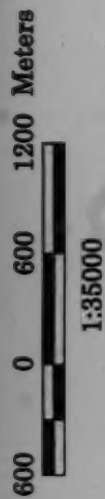
Latin Names	Common Names
<i>Ribes glandulosum</i>	skunk currant
<i>Ribes hudsonianum</i>	northern black currant
<i>Ribes lacustre</i>	black gooseberry
<i>Ribes oxycanthoides</i>	northern gooseberry
<i>Rosa acicularis</i>	prickly rose
<i>Rubus idaeus</i>	wild red raspberry
<i>Salix bebbiana</i>	beaked willow
<i>Salix commutata</i>	variable willow
<i>Salix drummondiana</i>	Drummond's willow
<i>Salix glauca</i>	grey-leaved willow
<i>Salix lucida</i> ssp. <i>lassiandra</i>	pacific willow
<i>Salix maccalliana</i>	Maccall's willow
<i>Salix planifolia</i>	tea leaved willow
<i>Salix pseudomonticola</i>	mountain willow
<i>Salix sitchensis</i>	Sitka willow
<i>Salix</i> species	willow species
<i>Sorbus scopulina</i>	western mountain ash
<i>Vaccinium membranaceum</i>	black huckleberry
<i>Vaccinium myrtilloides</i>	velvet-leaved blueberry
<i>Vaccinium vitis-idaea</i>	lingonberry
Mosses	
<i>Aulacomnium palustre</i>	glow moss
<i>Barbilophozia lycopodioides</i>	common leafy liverwort
<i>Brachythecium</i> species	ragged moss species
<i>Dicranum polysetum</i>	wavy-leaved moss
<i>Dicranum scoparium</i>	broom moss
<i>Dicranum undulatum</i>	wavy dicranum
<i>Drepanocladus aduncus</i>	common hook moss
<i>Drepanocladus uncinatus</i>	sickle moss
<i>Hylocomium splendens</i>	stair-step moss
<i>Lophozia ventricosa</i>	leafy liverwort
<i>Lycopodium annotinum</i>	stiff club-moss
<i>Lycopodium complanatum</i>	ground-cedar
<i>Pellia neesiana</i>	shiny liverwort
<i>Plagiomnium medium</i>	common leafy moss
<i>Pleurozium schreberi</i>	Schreber's moss
<i>Pogonatum alpinum</i> (<i>Polytrichum alpinum</i>)	stiff-leaved polytrichum
<i>Pohlia nutans</i>	copper wire moss
<i>Polytrichum commune</i>	common hair-cap
<i>Polytrichum juniperinum</i>	juniper hair-cap
<i>Polytrichum piliferum</i>	awned hair-cap
<i>Polytrichum strictum</i>	slender hair-cap
<i>Ptilium crista-castrensis</i>	knight's plume
<i>Rhizomnium glabrescens</i>	large leafy moss

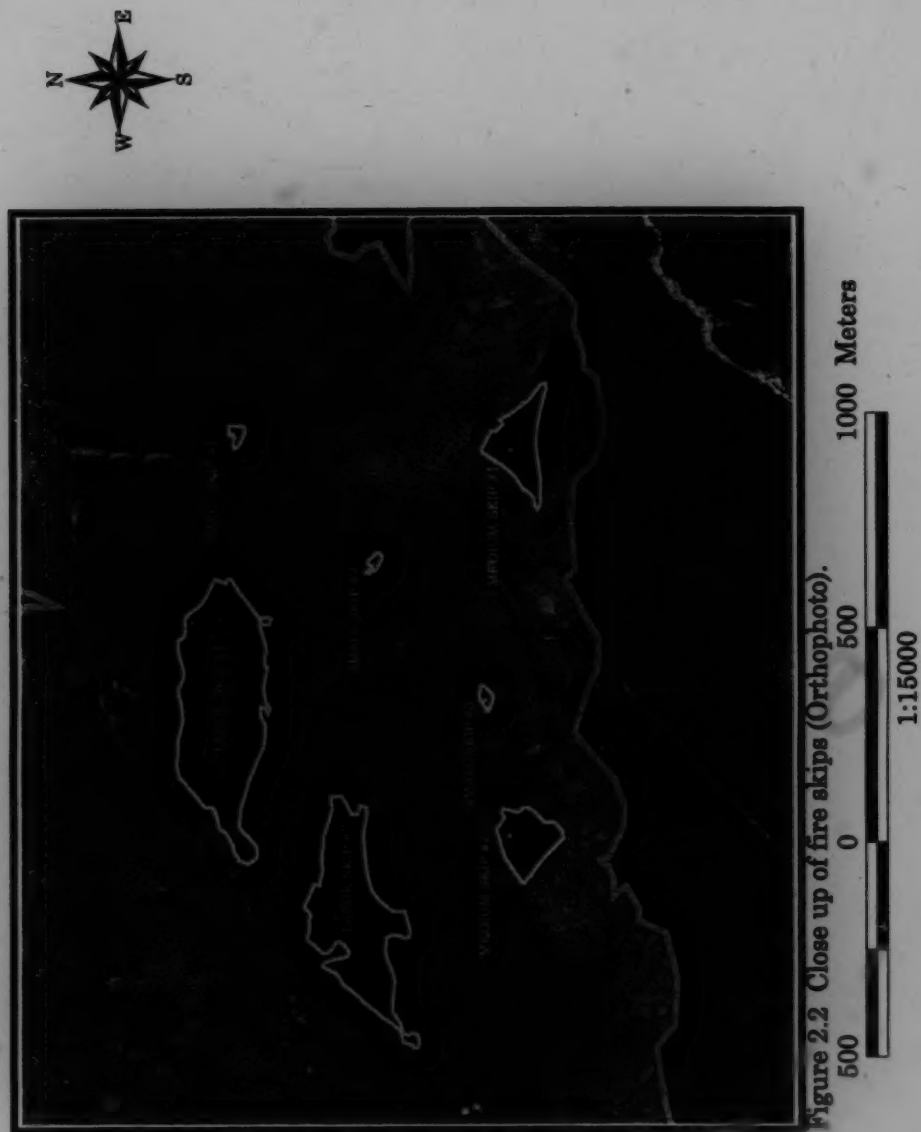
Table 2.10 Latin and common names of understory plant species (continued).

Latin Names	Common Names
<i>Sphagnum angustifolium</i>	poor-fen sphagnum
<i>Sphagnum fuscum</i>	common brown sphagnum
<i>Sphagnum girgensohnii</i>	common green sphagnum
<i>Sphagnum magellanicum</i>	midway peat moss
<i>Tomenthypnum nitens</i>	golden-fuzzy fen moss
<i>Tortula ruralis</i>	hairy screw moss
Lichens	
<i>Cetraria cucullata</i>	curled cetraria
<i>Cladina mitis</i>	green reindeer lichen
<i>Cladina rangerifera</i>	grey reindeer lichen
<i>Cladonia</i> species	club lichen species
<i>Icmadophila ericetorum</i>	fairies puke
<i>Lobaria linita</i>	lungwort
<i>Lobaria pulmonaria</i>	lungwort
<i>Peltigera aphosa</i>	freckled lichen
<i>Peltigera canina</i>	dog lichen
<i>Peltigera didactyla</i>	temporary pelt
<i>Peltigera leucophlebia</i>	freckled lichen
<i>Peltigera malacea</i>	apple pelt
<i>Peltigera neopolydactyla</i>	frog pelt
<i>Stereocaulon alpinum</i>	alpine coral lichen



Figure 2.1 Orthophoto of study site.





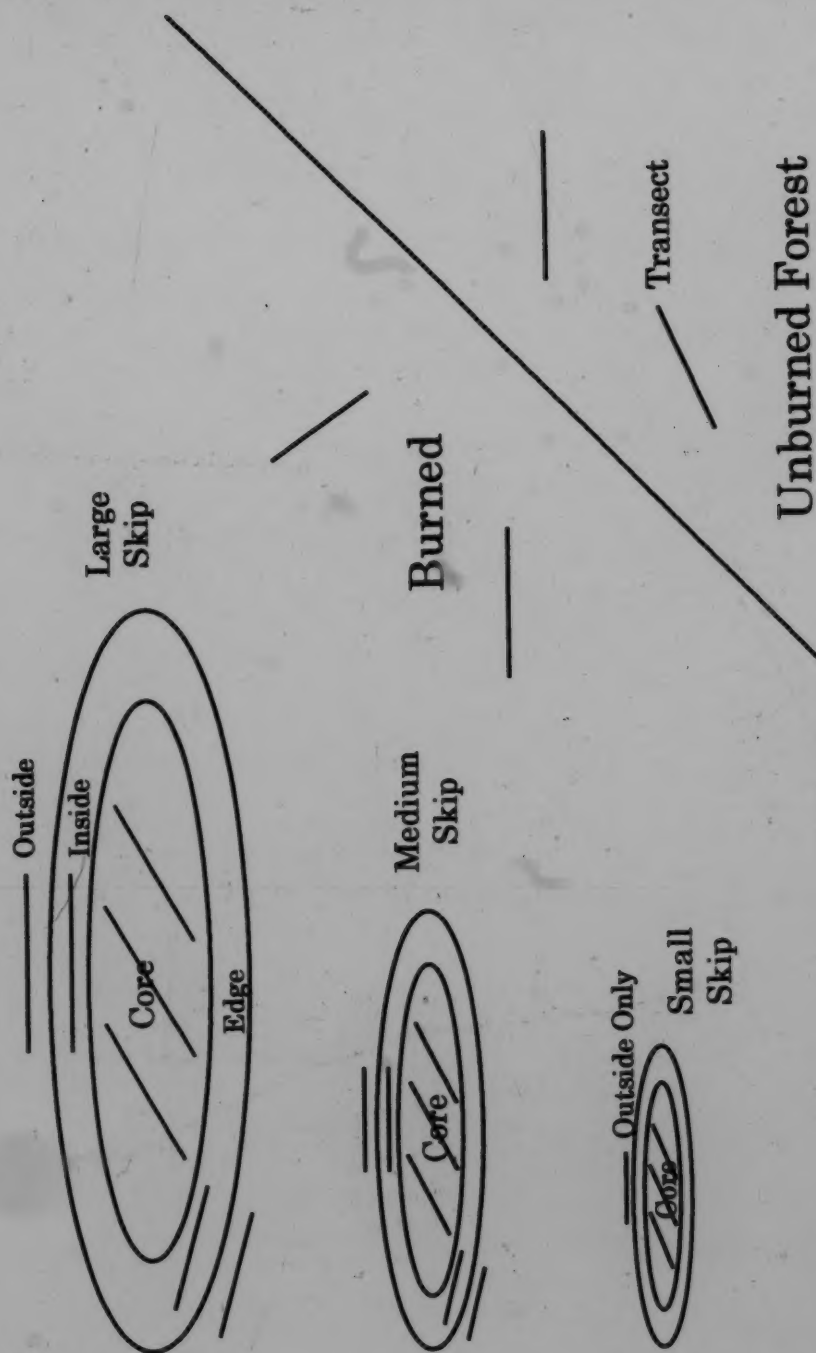
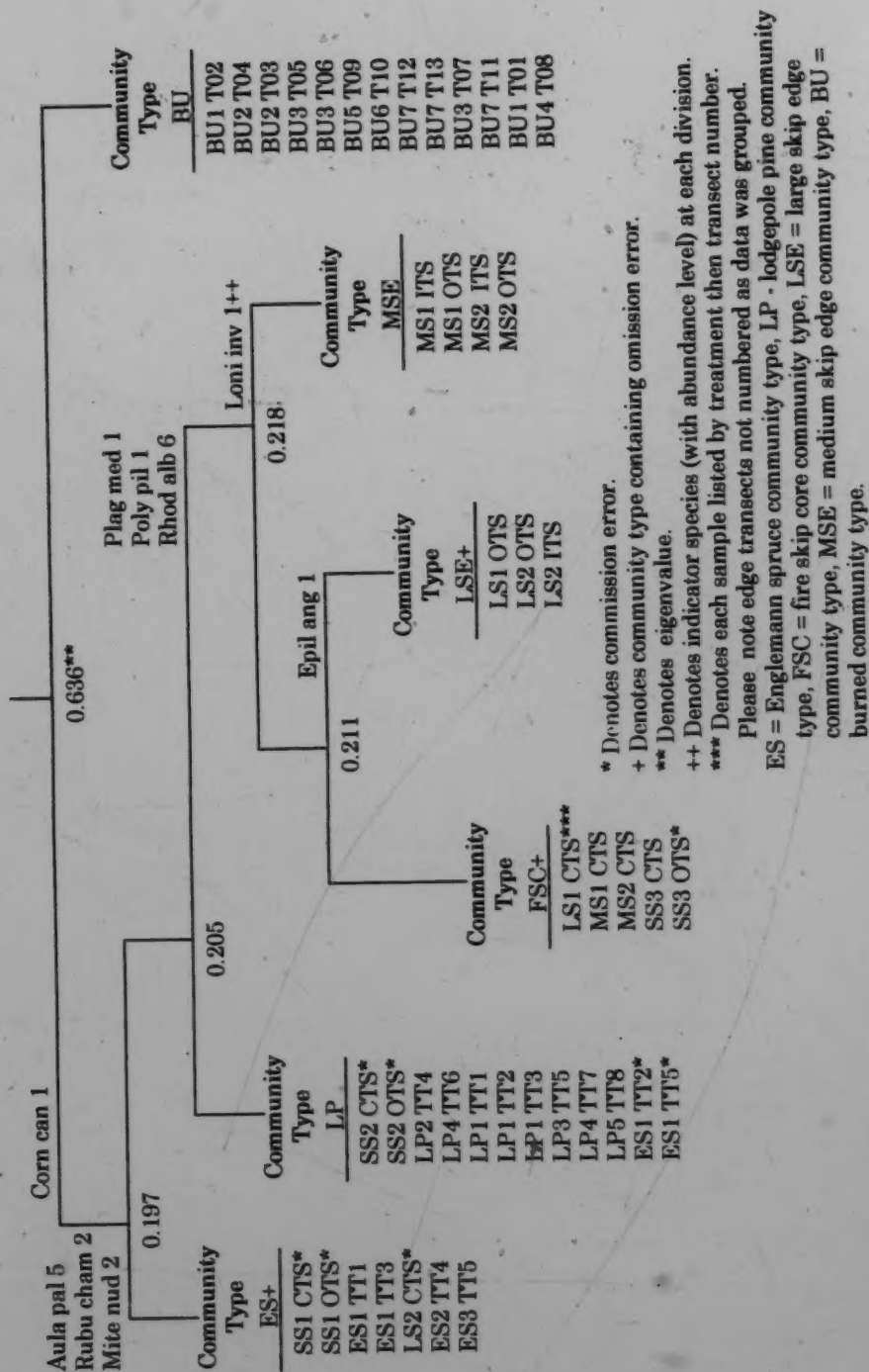


Figure 2.3 Diagram of treatment sampling (Not to scale).



* Denotes commission error.

+ Denotes community type containing omission error.

** Denotes eigenvalue.

++ Denotes indicator species (with abundance level) at each division.

*** Denotes each sample listed by treatment then transect number.

Please note edge transects not numbered as data was grouped.

ES = Englemann spruce community type, LP = lodgepole pine community type, FSC = fire skip core community type, LSE = large skip edge community type, MSE = medium skip edge community type, BU = burned community type.

Figure 2.4 Dendrogram of community types (groupings) obtained by TWINSpan.

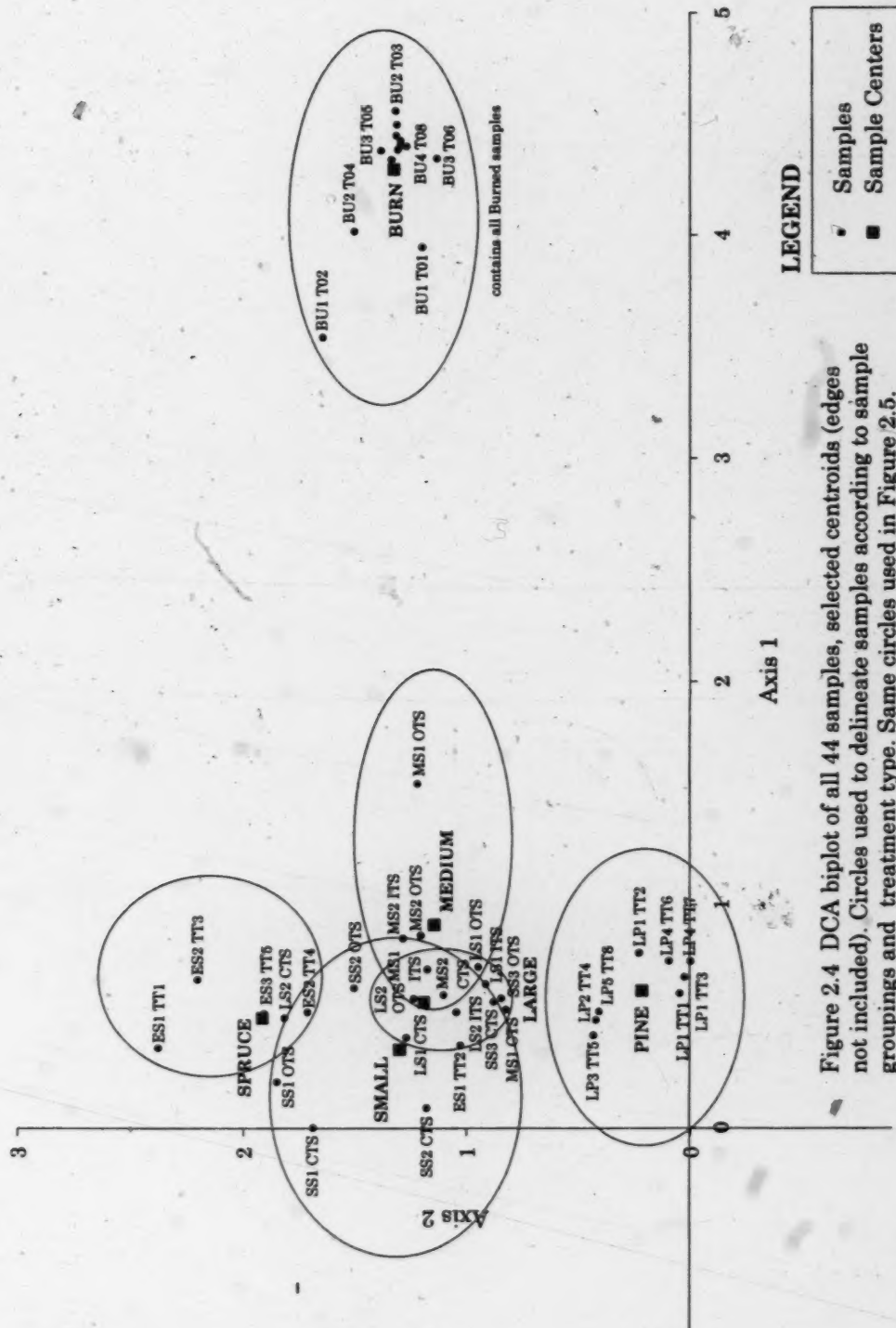
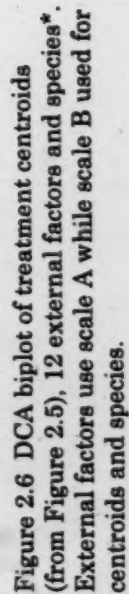


Figure 2.4 DCA biplot of all 44 samples, selected centroids (edges not included). Circles used to delineate samples according to sample groupings and treatment type. Same circles used in Figure 2.5.

LEGEND



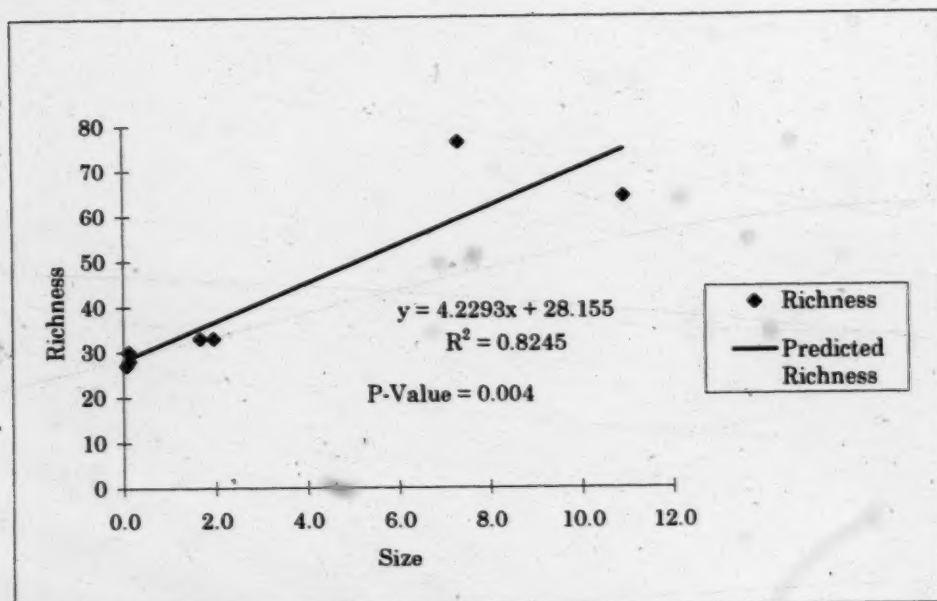


Figure 2.7 Linear regression of species richness of skips versus size of skips (95% Confidence Interval).

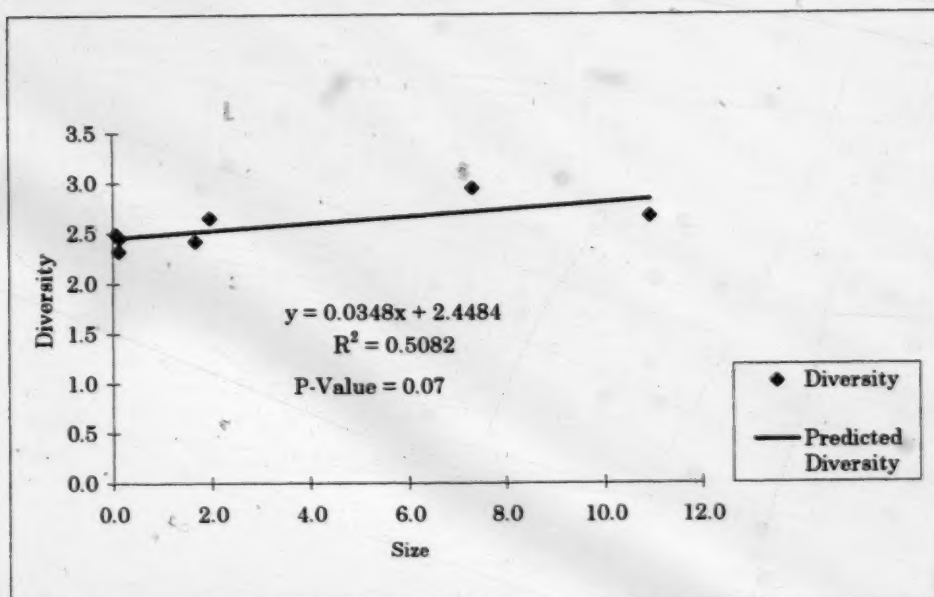


Figure 2.8 Linear regression of Shannon-Weiner species diversity versus size of skips (95% Confidence Interval).

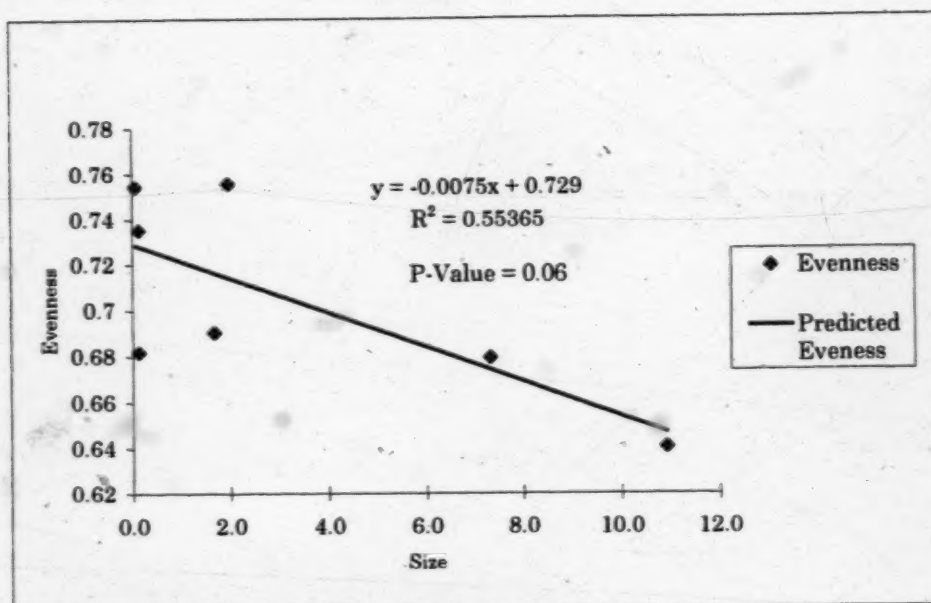


Figure 2.9 Linear regression of species evenness of skips versus size of skips (95% Confidence Interval).